Impacts of ship-induced waves on benthic macroinvertebrates

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Präsident
der Humboldt-Universität zu Berlin
Prof. Dr. Jan-Hendrik Olbertz

Dekan der
Landwirtschaftlich-Gärtnerischen Fakultät
Prof. Dr. Dr. h.c. Frank Ellmer

Gutachter : 1. Professor Dr. N. Walz

2. Professor Dr. K.-O. Rothhaupt

3. Dr. X.-F. Garcia

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Summary

Inland navigation constitutes a major human use of major rivers and lakes worldwide which is expected to increase in the future. Navigation does not only lead to river training and inputs of toxic compounds, but also significantly affects shore habitats by the ship-induced waves.

In contrast to the importance of such pressures, the effects of these hydrodynamic disturbances on benthic invertebrates in the littoral zones are poorly understood, even that invertebrates constitute a central element of littoral food webs. Hence, in this thesis I investigated i) the direct and immediate effects of ship-induced waves on benthic invertebrates in the littoral zone, ii) their subsequent effects on trophic interactions and iii) on the growth and fitness of invertebrates, and finally iv) the long-term effects on the community composition of benthic invertebrates in littoral zones.

Both laboratory and field experiments showed increasing detachment of invertebrates with higher wave-induced shear stress, following a sigmoid response curve. Detachment was significantly mitigated by higher structural complexity of some habitats, as complex habitats dissipate wave energy and provide better fixing possibilities for invertebrates. Moreover dislodgement of invertebrates resulted in an elevated risk of being preyed upon by fusiform fish. In contrast, deep bodied fish reduced feeding under wave disturbance. Waves also reduced the growth and energy storage of native invertebrates via reduced feeding rate or increased energy expenditure, while non-native invertebrates were not affected. The cumulative impact of the demonstrated various mechanistic effects of ship-induced waves alters the community composition of benthic invertebrates. The abundance of native invertebrates and total species richness was shown to be lower at sites exposed to ship-waves, while non-native invertebrates increased in abundance. Thus, ship-induced waves affect benthic invertebrates on the individual, species, and community levels, as well as the interaction of trophic levels, and hence will alter the ecological structure and function of whole littoral zones. This knowledge on the pathways how ship-induced waves affect littoral zones may be also used to develop scientifically based and target-oriented management plans for surface waters used as inland waterways. Adverse effects of ship-induced waves may be mitigated by specifically protecting structural complex habitats such as tree roots and dense reed belts, and by minimizing wave generation by increasing minimum sailing distance to shore or by adjusting vessel speed.

Zusammenfassung

Schifffahrt stellt weltweit eine der wichtigsten Nutzungen größerer Flüsse und Seen dar, die in Zukunft weiter zunehmen wird. Schifffahrt führt nicht nur zu Uferausbau und zum Eintrag toxischer Verbindungen, sondern beeinträchtigt außerdem die Uferhabitate durch den schiffsinduzierten Wellenschlag in erheblichem Maße.

Im Gegensatz zur Verbreitung dieser Beeinträchtigungen sind die Auswirkungen von Schiffswellen auf benthische Wirbellose jedoch bisher kaum bekannt, obwohl diese einen zentralen Bestandteil des litoralen Nahrungsnetzes darstellen. In der vorliegenden Arbeit untersuchte ich daher i) die direkten und unmittelbar wirkenden Effekte von Schiffswellen auf benthische Wirbellose, ii) die sich daraus ergebenden Auswirkungen auf trophische Interaktionen und iii) das Wachstum und die Fitness von Wirbellosen, sowie iv) die längerfristigen Veränderungen der litoralen Wirbellosengemeinschaften.

Die Labor- und Freilandversuche zeigten gleichermaßen, dass mit zunehmender wellengenerierter Sohlschubspannung mehr Individuen abgelöst und verdriftet wurden, wobei sich oft eine sigmoidale Verlaufskurve ergab. Der Ablösungseffekt wurde jedoch durch die hohe strukturelle Komplexität einiger Habitate gemindert, da hochstrukturierte Habitate die Wellenenergie stärker dissipierten und den Wirbellosen bessere Festhaltemöglichkeiten boten. Weiterhin führte die wellenbedingte Ablösung der Wirbellosen zu einem höheren Prädationsrisiko durch spindelförmige Fische. Im Gegensatz dazu reduzierten hochrückige Fische die Nahrungsaufnahme bei Wellenexposition. Wellenschlag verringerte außerdem das Wachstum und den Energiespeicher heimischer Wirbellosenarten, indem die Nahrungsaufnahme verringert oder der Energieverbrauch erhöht wurde, wohingegen Neozoen nicht beeinträchtigt wurden. Der kumulative Effekt der dargestellten Wirkungsmechanismen schiffsinduzierter Wellen veränderte die Artenzusammensetzung benthischer Gemeinschaften erheblich. Die Abundanz nativer Wirbellosenarten und die Gesamtartenzahl waren an wellenexponierten Uferbereichen geringer, während die Abundanz invasiver Arten anstieg. Folglich beeinträchtigen Schiffswellen benthische Wirbellose auf der Ebene der Individuen, Arten, Artengemeinschaften, sowie tropische Interaktionen, und können somit die ökologische Struktur und Funktion des gesamten Litorals beeinflussen. Dieses Wissen über die Wirkungspfade von Schiffswellen auf Uferzonen von Gewässern kann auch zur Entwicklung wissenschaftlich fundierter, zielorientierter Managementpläne für als Wasserstraßen genutzte Binnengewässer genutzt werden. Durch den gezielten Schutz komplex strukturierter Habitate wie Baumwurzeln und dichte Schilfbestände, sowie durch die Verminderung des Wellenschlags, durch eine größere Mindestabstände zum Ufer, und durch angepasste Fahrtgeschwindigkeit können die Beeinträchtigungen durch schiffsbedingten Wellenschlag abgemildert werden.

1 General introduction

1.1 Navigation – one of the major uses of freshwaters

Inland waters cover about 0.8% of the Earth's surface, but harbour almost 6% of all described species (Dudgeon et al. 2006), and thus represent focal sites of biodiversity. Moreover, they provide various ecosystem services for humans, such as offering freshwater supply, flood control and recreational areas (Millennium Ecosystem Assessment 2003). Due to the extensive use of these ecosystem services by humans, inland waters are subjected to numerous anthropogenic impacts particularly as human settlements are concentrated along shorelines (Strayer and Findlay 2010).

One of the oldest benefits for human societies living near surface waters is its use for navigation, both commercial and recreational. More than 600,000 km of waterways are used for inland navigation worldwide (Central Intelligence Agency 2011). In Europe, there are more than 36,000 km of navigable waterways (European Commission 2006). Germany has the longest network of navigable waterways (6,900 km) in Europe, followed by Finland (6,200 km) and France (5,900 km; European Commission 2006). The waterways in Germany represent 30% of the country's surface waters (Wolter 2001). These waterways are used for commercial and recreational navigation, with both sectors level off at a high level or slightly increase, even though the statistics of transport performance are subjected to annual fluctuation caused e.g. by the recent economical crisis (Tab. 1). A similar trend is also visible for waterborne traffic in the USA (US Army Corps of Engineers 2010). The transport performance of commercial navigation on European waterways was about 124.1 billion tkm in 2004, with more than half of it being transported via German waterways (63.7 billion tkm; European Commission 2006).

Table 1: Transport performance of German and USA inland navigation (Source: Statistisches Bundesamt Deutschland 2009; US Army Corps of Engineers 2010; Statistisches Bundesamt Deutschland 2011).

Year	Transport performance Germany (billion tkm)	Transport performance USA (billion short tmiles)
2004	63.667	341.2
2005	64.095	327.8
2006	63.975	334.4
2007	64.717	325.1
2008	64.057	312.6
2009	55.497	280.8
2010	62.278	No data

At present, about 12.7 million recreational boats are registered in the USA (US Department of Homeland Security and United States Coast Guard 2010) and more than 5.9 million boats are registered in the EU (pers. com. European Boating Association). For Germany, a number of 400,000 recreational boats is estimated (Dehn 2002).Within Germany, the rivers and lakes in the north-eastern lowlands comprise a focal area for recreational boating. The number of boats passing the locks in this area continues to steadily increase. Berlin is one of the most important regions for recreational boating in Europe, with 47,000 recreational boats and 27,000 passenger boats passing through lockings (Dehn 2002). In the adjacent federal states of Brandenburg and Mecklenburg-Vorpommern large numbers of recreational lockings are counted, too (e.g. Lock Fürstenber/obere Havel: 23,000 counted boats in 2001; Dehn 2002). Apart from a persistent increase in the number of (recreational) boats, the size and horsepower of vessels have shown a steep increase in the past three decades (Asplund 2003). Thus, inland navigation is an important and increasing socio-economic sector in Europe, with approximately 400,000 employees being directly or indirectly related to inland navigation in Germany alone (European Commission 2006).

1.2 Effects of navigation on aquatic ecosystems

There are numerous studies describing the degradation of water quality by navigation, and subsequent effects on aquatic organisms. Navigation is often accompanied by oil and fuel discharges (Jackivic and Kuzminsk 1973), as well as by the release of polyaromatic hydrocarbons (Mastran et al. 1994), which have toxic effects on aquatic organisms (Juttner et al. 1995). Antifouling paints containing Tributyltin (TBT), copper or booster biocides, have also been shown to have toxic effects on a wide range of non-target organisms, negatively affecting their growth, development, reproduction, survival and community composition. In addition, these compounds accumulate in the food web and may lead to regime shifts in lakes (Sayer et al. 2006; for further details see review by Dafforn et al. 2011). Because TBT is highly toxic to non-target organisms, it was banned in 2008, but is still present in sediments (Hedge et al. 2009; Dafforn et al. 2011). Furthermore, substitutes to this compounds are often also toxic and bioaccumulative (Mohr et al. 2009). Other chemicals, such as zinc, have been found to accumulate in mussels (Young et al. 1979), and lead to changes in epifaunal assemblages in response to marina operations and boating activities (Turner et al. 1997).

Only recently, the role of inland navigation in facilitating the dispersal of non-native aquatic species has been recognised as another major impact on aquatic ecosystems. The invasion of non-native species is considered as one of the most serious threats to global

biodiversity (Sala et al. 2000; Secretariat of the Convention on Biological Diversity 2006). The construction of canals between river systems, such as the Rhine-Main-Danube canal, connects catchments that were previously separated by biogeographical boundaries (bij de Vaate et al. 2002; Nehring 2005; Leuven et al. 2009). Such connections greatly facilitate the exchange, and possibly the homogenisation, of aquatic fauna (e.g. Kinzelbach 1995; Pysek et al. 2010; Strayer 2010), which often results in a loss of biodiversity ((e.g. Kaufman 1992; McKinney and Lockwood 1999; McKinney 2002; van der Wal et al. 2008) (but see Rahel 2002; Piscart et al. 2010)). Navigation may even directly support species invasions, as vessels may transport and disperse non-native species within their ballast water or via hull attachments (Mills et al. 1993; Duggan et al. 2005; Nehring 2005; Hulme et al. 2008; Leuven et al. 2009). Transport within ballast water even allows the inter-continental transfer of freshwater species (bij de Vaate et al. 2002).

When natural rivers and lakes are used as navigable waterways their morphology becomes significantly altered as a result of river training, which includes the deepening and widening of the river channel, the steepening and artificial protection of shores, or impoundment via locks generate considerable uniformity in habitats and food webs (Brauns et al. 2011), with typical riverine habitats tending to be replaced by lentic or artificial habitats. Other physical impacts emerge from anchored or moored vessels, as moorings were shown to depauperate benthic invertebrate communities (Lenihan et al. 1990) and to affect submerged vegetation (Hastings et al. 1995; Ostendorp 1999). The generation of noise from propellers and motors associated with moving vessels increases stress levels and heart rates of fishes, and may even lead to significant changes in their sensory and hearing capabilities (Scholik and Yan 2002; Wysocki et al. 2006; Graham and Cooke 2008). In addition, direct contact with hulls and propellers may injure aquatic fauna (e.g. Bulte et al. 2010), and may affect macrophyte stands by creating lanes that are still visible after 2-5 years (Zieman 1976).

1.3 Hydrodynamic effects of navigation

The most pronounced direct physical effect of navigation is the alteration of the local hydrodynamic regime i.e. the generation of currents and ship-induced waves. When a vessel moves across a water body it displaces water and pushes it in front of it, leading to increased pressure and the generation of a front wave (Fig. 1). The increased difference in static pressure between the bow and the stern accelerates the water passing underneath and around the ship. Static pressure rises in the vicinity of the bow, then falls below the free stream pressure at the midsection of the vessel, and rises again near the stern. The water surface

profile along the hull responds to this pressure distribution by causing the water surface to rise at the bow and stern and to fall and accelerate water along the midsection (Sorensen 1997). In spatially confined waterways, the resulting swell and down-surge cause return currents and drawdown at the banks (Fig. 1). Behind the ship the pressure equalises with the undisturbed water level, thus creating the stern wave. The aforementioned pressure changes are termed the primary wave system. Primary waves appear most pronouncedly in the vicinity of ships, and thus particularly affect the shorelines of waterways that are confined in water depth and width.

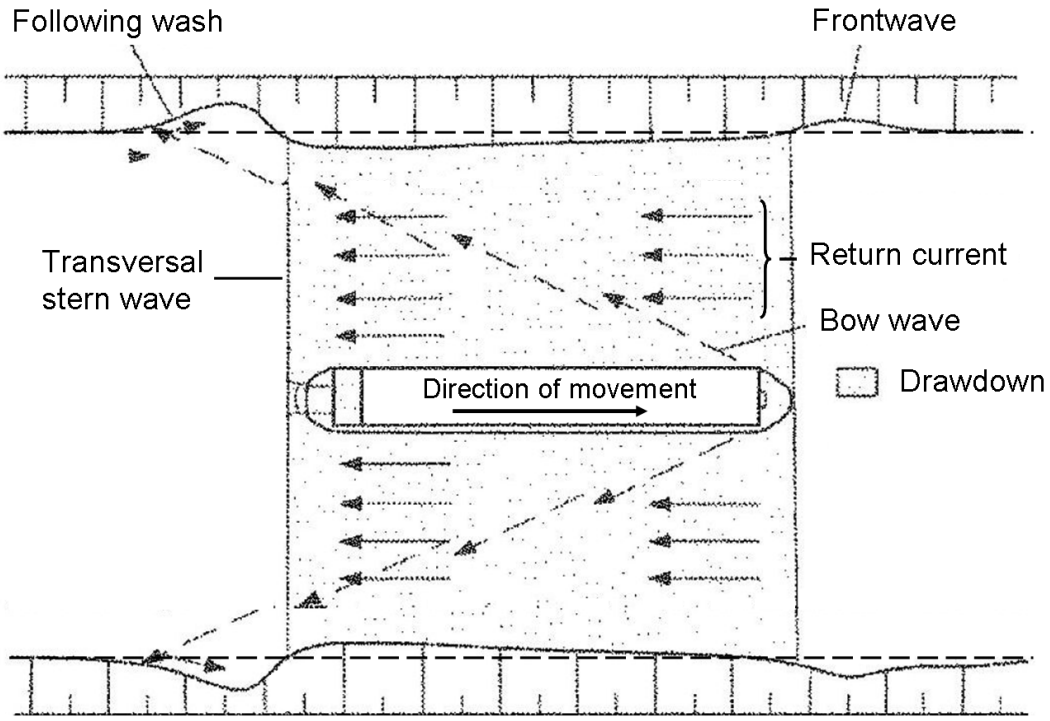

Figure 1: Wave field of a vessel sailing in restricted waters (adapted from Oebius 2000).

Inertia causes the water surface to lag behind its equilibrium position and produces a surface oscillation when responding to the sharp pressure gradients at the bow (and possibly at the stern), which induces a rapid rise and fall in the water surface. This in turn produces the pattern of free waves that propagate out from the vessel and follow it (Fig. 2; Sorensen 1997). This wave pattern is commonly termed the secondary wave system. This system consists of two different trains of waves, diverging (moving forward and out from the vessel) and transversal waves (following the course of the vessel at a right angle), which are created at the bow and usually, to a smaller extent, at the stern of the ship. Diverging and transversal waves can interact with and superimpose each other. While the primary wave system mainly occurs in the vicinity of the ship and, hence, is more important in confined waterways, the secondary wave system reaches distances further away from the ship and, thus, may even reach and

affect the shores of larger waterways and lakes (Söhngen et al. 2008). Also primary and secondary wave systems can interact and superimpose each other.

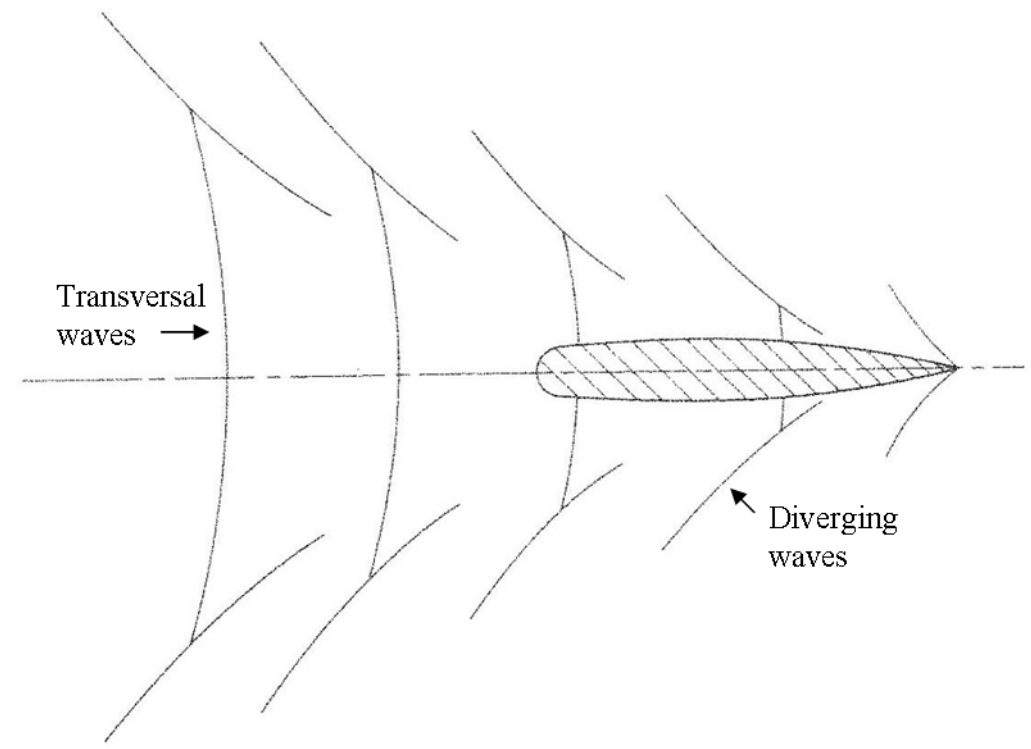

Figure 2: Transversal and diverging waves of a vessel sailing in deep water (adapted from Sorensen 1973).

The properties of ship waves, such as wave height, wave length or the celerity of the waves, result from ship characteristics and the morphology of the waterway. The hull form, length and draught of the vessel, and especially its speed determine wave parameters. As the travel velocity of a vessel increases, wave height also increases until the vessel reaches super critical speed and starts planing, which means that it is riding on its front wave. This transition from displacement to planing mode only marginally increases wave height (Maynord 2005). However, large commercial vessels travelling in confined waterways such as canals, rarely reach planing mode, due to speed limitations and ship performances (Söhngen et al. 2008). In confined waterways, the flow acceleration and resulting pressure gradient due to ship passage, is greater than in wide and deep water bodies (Sorensen 1997). As the waves dissipate with distance from the ship, the distance between the sailing ship and the shore is particularly important in determining the intensity of wave action on the shore. In addition, ship waves are strongly influenced by water depth. When waves reach shallow water (defined as a water depth that is less than half of the wave length), they are affected by the bottom. As the water

becomes shallower, the wave length becomes shorter and the wave becomes faster and grows higher and steeper until it breaks.

1.4 Effects of ship-induced waves on shores

In contrast to naturally occurring wind-induced waves, ship-induced waves also reach shorelines that are protected from the wind. Furthermore, ship-induced waves occur in a stochastic and abrupt way, whereas wind-induced waves including those of great heights will grow gradually with increasing wind velocity, wind duration and fetch length. In water bodies with restricted fetch, ship-induced waves may reach greater wave heights than wind waves and, occur more frequently than waves resulting from strong wind events. For example, ship-induced wave heights of up to 0.6 m and 0.5 m were measured in the Mississippi River (Bhowmik et al. 1991) and Lake Constance (Hofmann et al. 2008). These extreme wave heights occur more often for ship-induced waves than for wind-induced waves (Bhowmik et al. 1982; Hofmann et al. 2008). In addition, ship-induced waves have a greater effect on sediment resuspension than wind-induced waves (Schoellhamer 1996).

Ship-induced waves have been shown to affect various components of aquatic ecosystems (Table 2) with subsequent and interacting effects on other components. Some of the first and most intensively studied effects of ship-induced waves are shoreline erosion and sediment resuspension (Table 2). Sediment resuspension leads to increased turbidity, with subsequent effects on macrophyte growth and primary production (Table 2). In addition, the distribution of dissolved compounds in the water mass as well as water chemistry is modified by ship-induced waves. Macrophytes are directly affected by wave disturbance resulting in mechanical damage and shifts in the composition of communities. Most of the studies investigating the effects of ship-induced waves on aquatic fauna have focussed so far on fish. For example, there are several studies demonstrating the effects of waves on the eggs, larvae and juveniles of fish (Table 2).

Bishop (2004) provided first evidence for alterations of benthic invertebrate assemblages caused by ship-induced waves generated by ferries. Comparing the benthic infaunal community compositions of wash and no-wash zones in a tidal Australian river, she found lower abundances of some polychaete species in the wash zones, while other groups were less affected. Furthermore, the abundance of Polychaetes increased when the ferry service was abandoned for 9 weeks (Bishop and Chapman 2004). However, the applicability of these results to invertebrate epifauna and freshwater environments remained unclear. While infauna mostly does not directly experience wave induced disturbance and might be protected in the

sediments, for epifauna greater effects of wave disturbance are expected as they are more directly exposed to hydrodynamic disturbance.

In addition, it has been demonstrated that ship-induced waves can detach invertebrates from seagrass blades (Bishop 2008). Thereby, it has been shown that even a small vessel can displace invertebrates from flapping seagrass blades, reducing species abundances and richness for at least one hour after disturbance. However, only one level of disturbance has been applied, and hence the results do not allow quantitative disturbance-response relationships to be derived.

Scheifhacken (2006) showed that pulsed waves reduced the growth of the lentic snail *Radix ovata*, particularly in shallow waters.

Table 2: Effects of ship-induced hydrodynamic alterations on aquatic ecosystems.

Compartment compounds	**Ecological effects**	**References**
Sediment	Shoreline erosion, sediment resuspension, increased turbidity	(Garrad and Hey 1987; Nanson et al. 1994; deWit and Kranenburg 1997; Cyr 1998; Environmental agency 1999; Anthony and Downing 2003)
Chemical compounds	Increased release of methane, oxygen depletion, changes in chemicals and nutrient distribution	(Hofmann et al. 2010) (Hamilton and Mitchell ; Yousef et al. 1980; Asplund 1996; Hamilton and Mitchell 1997; Anthony and Downing 2003)
Macrophytes	Uprooting, mechanical damage, growth limitations, changes in community composition, shading due to increased turbidity affects macrophyte development	(Cragg et al. 1980; Liddle and Scorgie 1980; Ostendorp 1989 and references therein; Vermaat and Debruyne 1993; Coops et al. 1996; Ali et al. 1999; Doyle 2001)
Fish	Increased mortality of eggs and larvae, reduction of swimming performance, increased stranding, reduced spawning, reduced growth	(Sutherland and Ogle 1975; Holland 1986; Adams et al. 1999; Arlinghaus et al. 2002; Wolter and Arlinghaus 2003; Wolter et al. 2004; Stoll and Fischer 2011)
Macroinvertebrates	Decreased abundance of infaunal species, dislodgement of epifaunal species, reduced growth of snails	(Bishop 2004; Bishop and Chapman 2004; Scheifhacken 2006; Bishop 2007, 2008)

1.5 Approach and aims of this thesis

As shown, current knowledge about the impact of ship-induced waves on benthic invertebrates is extremely limited. Understanding this relationship is nevertheless essential, since benthic invertebrates constitute a significant portion of total biodiversity, and play a key role in the metabolism of matter in aquatic systems. Specifically, invertebrates transfer carbon and energy from primary producers and detrital deposits to higher trophic levels in littoral food webs (Cuffney et al. 1990; Wallace and Webster 1996). Invertebrates are ideal indicators of anthropogenic influences and disturbance effects, because of their sedentary nature, relatively long life histories, diversity, sensitivity to changes in their environment and their ubiquitous distribution (Rosenberg and Resh 1993; Abel 1996). The existence of relatively large numbers of invertebrate species offers a wide spectrum of responses to different kinds of stress (Hellawell 1986) such as hydrodynamic disturbances.

Within the framework of this thesis, I aimed to contribute towards obtaining a better understanding of the effects of ship-induced waves on littoral macrozoobenthos. To elucidate the underlying mechanisms of this relationship, laboratory and field based experimental investigations were used, in addition to field surveys, focusing on wave effects at individual and community levels, as well as the interaction between trophic levels. In the present thesis, I studied immediate, subsequent and long-term effects of ship-induced waves on littoral macroinvertebrates. The main components of this thesis comprised the following:

- Direct and immediate effects of ship-induced waves were investigated in an experimental wave flume (Chapter 2) and under field conditions (Chapter 3), in order to establish quantitative relationships between invertebrate dislodgment and wave-induced disturbance. It was hypothesised that with increasing wave-induced shear stress more individuals would be detached from their habitats, and that this effect would be mitigated by a high degree of structural complexity of habitats.
- When invertebrates are detached from their habitats they hurled through the water column for a while before being able to clink to a habitat again. The detachment of invertebrates from their protective habitats could increase the risk of fish predation. This assumption was tested via laboratory experiments in cooperation with the Limnological Institute of the University of Constance under three scenarios: pulse waves (simulating ship-induced waves), continuous waves (simulation wind waves) and a no wave control. By quantifying foraging attempts, foraging success and swimming activity of fish predators and the suspension rate of their benthic prey, the following hypotheses were tested: i) waves increase prey accessibility, especially under pulse

waves as sudden disturbance detaches more invertebrates, ii) smaller fusiform fish benefit more from hydraulic stress than larger or deep bodied fish, and iii) ship-induced waves have a stronger impact on predator-prey interactions than wind-induced waves (Chapter 4).

- Repeated disturbance by ship-induced waves could result in higher activity rates and higher energy demands of benthic invertebrates. During a 6 week laboratory experiment, the growth rates of invertebrates of wave exposed individuals and individuals in a control flume without waves were compared. Since invasive invertebrates can disperse by attaching to the hulls of ships or in the ballast water of vessels, and often spread via and efficiently colonize navigable waterways, it was hypothesised that non-native invertebrates are less susceptible to ship-induced wave disturbance than native invertebrates, with respect to growth rates, energy storage and mortality (Chapter 5).
- The strong immediate effects and subsequent after-effects of waves could lead to long-term changes in the composition of the benthic community by favouring or excluding a subset of invertebrate species. Comparing the composition of benthic communities along a wave exposure gradient (high exposure, intermediate exposure and reference sites), it was hypothesised that ship-induced waves alter the community composition of benthic invertebrates, and favour non-native species. These effects are expected to be more pronounced in habitats with low structural complexity (Chapter 6).

The main results, perspectives and implications of this thesis are summarised and discussed in the general discussion section (Chapter 7).

2 Resistance to ship-induced waves of benthic invertebrates in various littoral habitats

Friederike Gabel, Xavier-François Garcia, Mario Brauns, Alexander Sukhodolov, Marc Leszinski and Martin T. Pusch

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Summary

1. Ship-induced waves disturb benthic invertebrate assemblages colonising littoral zones of lakes and rivers. However, the impact of ship-induced waves on invertebrates has rarely been quantified, and the influencing factors have not been addressed.

2. In an experimental wave tank, five benthic invertebrate species, *Bithynia tentaculata, Calopteryx splendens*, *Dikerogammarus villosus, Gammarus roeseli* and *Laccophilus hyalinus*, were exposed to waves of increasing shear stress (0.43 to 2.19 N m^{-2}). Mean number of detached individuals was recorded for five littoral habitats [coarse woody debris (CWD), reeds, tree roots, sand and stones], representing different levels of structural complexity as quantified by their fractal dimensions (FD).

3. Results showed that detachment of invertebrates was significantly related to shear stress in all habitats except tree roots. Detachments averaged for the five species were significantly lower in habitats with a high degree of structural complexity, decreasing in the habitat sequence: sand, CWD, stones, reeds and tree roots.

4. Consistent with their different morphologies and methods of attachment to substrates, the five species displayed differences in their response to hydraulic stress that were dependent on habitat.

5. The increasing sheltering effect of structural habitat complexity was mirrored by increasing dissipation of the kinetic energy of waves; i.e. the FD of the habitat was positively correlated with shear stress reduction due to the flow resistance of the habitat.

6. Network habitats such as tree roots provided the best sheltering conditions against hydraulic disturbance, because they combined good refuge availability for all studied

invertebrate species and maximal dissipation of kinetic wave energy. Consequently, persistent anthropogenic impacts, such as lakeshore modification or long-term exposure to ship-induced waves, which cause disappearance of complex littoral habitats such as tree roots or dense reed belts, will drastically increase the adverse effects of boating and ship traffic on littoral invertebrate assemblages.

2.1 Introduction

Wind-induced waves are a key determinant of habitat conditions at wind-exposed shores of lakes. Wind exposure maintains stony bottoms by preventing sediment accumulation (Brodersen 1995; James et al. 1998; Tolonen et al. 2001), which generally favours high diversity and abundance of benthic invertebrates (Cardinale et al. 1997; Abdallah and Barton 2003). Ship-induced waves produced by freight barges, passenger ships and recreational boats constitute a major additional hydraulic disturbance for invertebrates in the littoral zones of lakes, rivers and canals used as inland waterways. Although organisms at wind-exposed shores may be adapted to a regime of strong hydrodynamic forces, ship-induced waves are characterised by strong amplitudes and short-term increase of flow velocity (Bhowmik and Mazumder 1990; Rodriguez et al. 2002) and boat wakes can introduce waves to otherwise sheltered habitats where organisms are poorly adapted to hydrodynamic forces.

Very few published studies have documented the impact of ship-induced waves on shore assemblages. Studies of estuarine invertebrates have indicated that hydrodynamic regime and not sediment characteristics drive differences between invertebrate assemblages of wash and no-wash zones (Bishop 2004; Bishop and Chapman 2004; Bishop 2005, 2007). Bishop (2003), found lower abundances of gastropods and amphipods on sea grass blades exposed to ship-induced waves, and suggested that invertebrates were detached by the flapping of the blades as wave propagates. In the littoral zone of navigable rivers, ship-induced waves evidently constitute a major impact on macroinvertebrate communities (Brunke et al. 2002; Garcia et al. 2006) and on young fish (Holland 1986; Wolter and Vilcinskas 1997; Arlinghaus et al. 2002; Wolter and Arlinghaus 2003). Mainly, organisms are expected to be relocated, but also to suffer from mechanical injuries caused by shear stress, increased expenditure of metabolic energy for swimming, oxygen depletion due to sediment resuspension and increased risk of predation.

However, little is known about potential thresholds in the response of littoral invertebrates to anthropogenic wave disturbances of increasing shear stress, or about the interaction with habitat properties. In particular, the factors influencing the extent to which invertebrates are

detached by waves in specific littoral habitats have never been addressed. The only published evidence comes from a related case with stream invertebrates exposed to continuous flow in flume experiments, which demonstrated that current-induced drift of lotic invertebrate species increased with increasing flow velocities (Borchardt 1993; Imbert and Perry 1999), and that the proportion of drifting individuals decreased when woody debris was added to a sand habitat (Borchardt 1993).

As the global navigation network constantly expands (see Revenga et al. 2000), and recreational boating increases, quantitative information about the impacts of ship-induced waves is urgently needed to develop scientifically-based recommendations for shoreline management in navigable water bodies. We therefore investigated the resistance of invertebrates to ship-induced waves in relation to the structural complexity of littoral habitats. Five benthic macroinvertebrate species, representing a spectrum of body morphologies and attachment strategies, were successively exposed to waves of increasing shear stress in five habitats exhibiting different structural complexity. We hypothesized that (i) the proportion of detached individuals depends on the level of shear stress associated with the wave; (ii) the proportion of detached individuals also depends on species-specific adaptations to certain habitats, and (iii) the number of detached individuals decreases with greater habitat structural complexity.

2.2 Material and Methods

Experimental system

Experiments were conducted in an experimental wave tank 3.0 m long, 0.80 m wide and 0.60 m deep made of 10 mm thick Perspex panels (Fig. 3). Waves of different shear stress were produced with a flap wave maker (Dean and Dalrymple 1984), by varying the water level in the wave tank and the weights used to move the flap-plate.

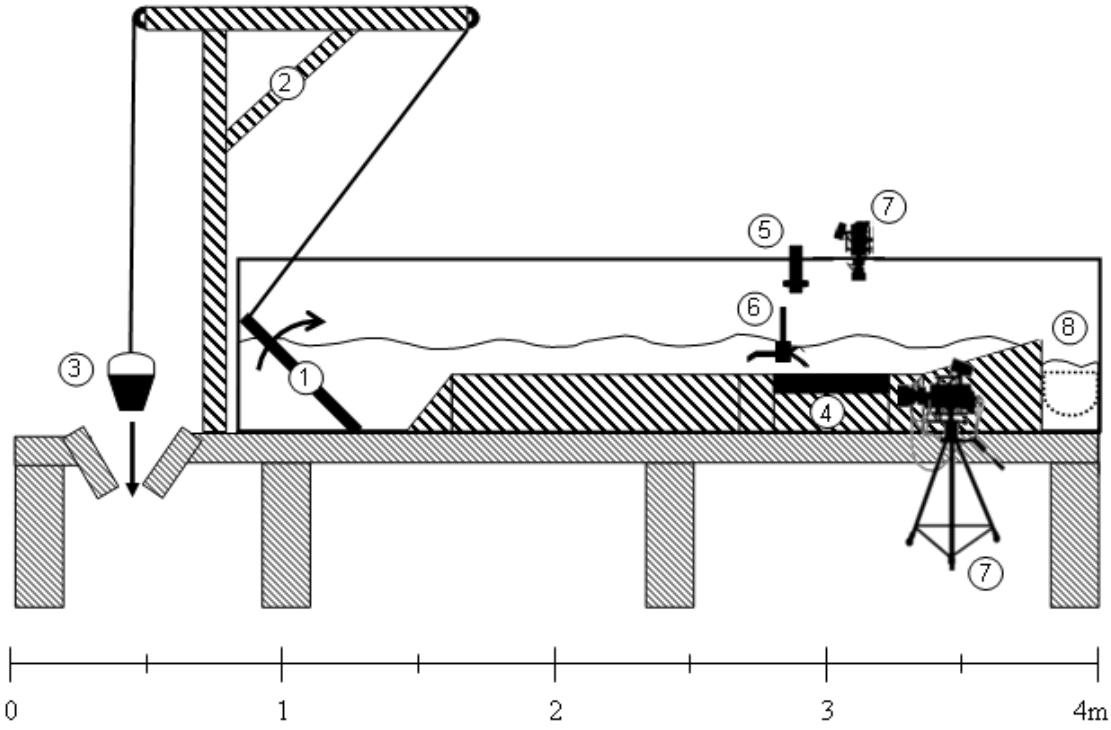

Figure 3: Sketch of the experimental wave tank. Wave maker system: flap-plate (1), gibbet (2), bucket with varying-weight (3). Observation area: removable habitat trays (4), acoustic wave sensor (5), acoustic Doppler velocimeter (6), video camera (7), discharge basin with net (8).

In the observation area, two removable plastic trays each of 0.115 m² area and filled with sand, were placed side by side, in which the various habitats were exposed to waves. At the far end of the tank a slope with an angle of 20° and a discharge basin covered by a net were added to prevent reflection of the waves against the tank wall. The net collected invertebrates that were flushed from the observation area by the wave. Sand was glued on the plates 40 cm in front and behind the habitat trays to avoid any hydraulic perturbations in the study area due to changes in roughness along the wave route.

Hydrodynamic characteristics of the waves were measured by electronic devices installed in front of the habitat trays on the right side of the tank. Wave height was recorded with an acoustic wave sensor (UltraLab USS2001300, General Acoustics, 20 Hz recording, Kiel, Germany) located 50 cm above the water level. Flow velocity was recorded using an Acoustic Doppler velocimeter (Micro ADV 16 MHz, Sontek, 50 Hz recording, San Diego, CA, U.S.A.) with the sampling volume positioned 1 cm above the flow bed. This location was the closest location to the bottom allowed by the technical characteristics of the ADV for measurements of flow velocities faced by invertebrate species. We assumed that bottom boundary layer is thinner than the body height of the flattest invertebrate species studied so that flow velocities measured by the ADV are those really faced by invertebrates. The proportion of benthic

invertebrates disturbed by the experimental waves was assessed by counting the number of individuals detached from the habitat, using video records from two cameras located on the top and on the right side of the study area (Fig. 3).

Shear stress calculation

The bottom shear stress τ (N m^{-2}) caused by the wave at the location of the habitat trays was calculated as:

$$\tau = 0.5 f \rho U_b^2 / 10$$

where ρ is the density of water (1 g cm^{-3}), U_b (cm s^{-1}) is maximum wave orbital velocity (measured by the ADV) and f is the wave friction factor. The null values recorded for the vertical and lateral components of the maximum wave orbital velocity indicated that the flow in the wave tank was unidirectional. In addition, Reynolds numbers for the experimental flow calculated as

$$\mathrm{Re} = \frac{ul}{v}$$

where u is the maximum wave velocity behind the different habitats (maximum 43 cm s^{-1}), l is defined as the wave amplitude (Dyer 1986) (maximum 4 cm) and ν is water viscosity (*c.* 0.01 cm^2 s^{-1}), were about 10^4, which is one order of magnitude lower than the critical value reported by (Jensen 1989) for turbulent flows on smooth beds. Hence, shear stress at the front of the habitat tray was mainly produced by mean flow since according to calculated Reynolds numbers, no significant turbulences were generated. Consequently, the wave friction factor was calculated according to the formula given by Dyer (1986) for laminar flow:

$$f = 2\sqrt{\frac{\nu}{U_b A_b}}$$

where A_b (cm) is the maximum bottom wave amplitude (measured by the acoustic wave sensor).

Flow conditions in the wave tank

Single waves (soliton) were generated in the wave tank in order to simulate the first wave of a characteristic ship-induced wave train hitting the habitats. In natural conditions, the first wave of a characteristic ship-induced wave train is expected to have the greatest effects on invertebrates because of its highest amplitude and sudden appearance. We thus used solitons since they are technically easier to produce in an experimental wave tank than a wave train.

Using combinations of eight different weights and two water levels, waves of 10 different shear stress levels were produced in the experimental wave tank. Resulting shear stress values at the location of the habitat trays ranged from 0.45 to 2.19 N m^{-2} (Table 3), and were significantly different from each other (ANOVA with Scheffé post hoc test, n = 100, lowest significance level: P = 0.023; Table 3). The observed coefficient of variation for all combinations was low, ranging from 0.36% to 2.17% (Table 3), indicating that a given combination of weight and water level generated waves with similar hydraulic characteristics.

Table 3: Flow conditions in the wave tank. For each shear stress level applied (combination of bucket weights and water depths), the respective wave height and velocity, as well as the calculated shear stress value (mean ± SE) with its coefficient of variation (CV, n=10) is given. The level of significance (*P*) refers to the test of differences between two consecutive shear stress levels (ANOVA, Scheffé's post hoc, n=10).

Weight (kg)	Water depth (cm)	Wave height (cm)	Wave velocity (cm s^{-1})	Shear stress (N m^{-2})	*P*	CV (%)
8	15	1.50 ± 0.02	11.18 ± 0.06	0.432 ± 0.002	<0.001	2.17
10	15	2.50 ± 0.03	19.29 ± 0.11	0.751 ± 0.003	<0.001	1.55
12	15	3.64 ± 0.03	28.16 ± 0.01	1.111 ± 0.004	<0.001	1.13
14	15	4.85 ± 0.03	33.74 ± 0.09	1.254 ± 0.004	<0.001	1.50
16	15	6.45 ± 0.04	39.32 ± 0.11	1.369 ± 0.004	<0.001	1.00
18	15	6.92 ± 0.04	42.37 ± 0.10	1.483 ± 0.003	0.013	0.81
20	15	7.42 ± 0.04	45.22 ± 0.10	1.579 ± 0.002	0.023	0.39
22	15	7.96 ± 0.04	47.45 ± 0.10	1.636 ± 0.003	<0.001	0.54
10	10	5.00 ± 0.04	46.29 ± 0.09	1.985 ± 0.005	<0.001	0.74
12	10	5.44 ± 0.03	50.85 ± 0.13	2.189 ± 0.005		0.36

The waves produced in the wave tank (wave heights ranging from 1.5 to 8 cm and maximum orbital velocities from 11 to 50 cm s^{-1}) were comparable with wave characteristics induced by small private boats (wave heights 4.5-8.8 cm, maximum orbital velocities of 21 - 44 cm s^{-1}) as measured on Lake Langer See and the River Spree, Berlin, Germany (D. Franke, unpubl. data).

To assess the spatial homogeneity of the hydraulic conditions at location of the habitat trays, 10 repeated measurements of wave characteristics were conducted on both the left and right sides of the tank for two different shear stress levels (0.43 and 1.37 N m^{-2}). No significant differences in maximum wave orbital velocities, wave heights or calculated shear stress values were found between the two sides (ANOVA, n = 10 per test, $P > 0.05$ for all tests). Consequently, all experiments were conducted with the electronic devices fixed on the right side of the wave tank. Similarly, no significant differences in flow velocities were found

at different depths along the vertical profile (measured each subsequent centimetre from 1.0 to 8.0 cm above the flow bed for 10 replicated waves of 1.37 N m^{-2}, ANOVA with Scheffé post hoc test, n = 90, $P > 0.05$), indicating that the flow generated by the waves in the experimental wave tank was vertically uniform above bottom boundary layer and that the measurement point of 1 cm distance to the bottom is representative for the flow.

Habitat trays

Five habitats [coarse woody debris (CWD), reeds, sand, stones and tree roots] commonly found in the littoral zone of north-east German lakes were used for the experiments. Structural elements used in the simulations of the five habitats were collected from regional lakes, and arranged in the removable trays on a 2 cm thick layer of sand, respecting design and densities observed under natural conditions. The CWD habitat tray consisted of two flat pieces of ridged bark of about 400 cm^2 each. The reed (*Phragmites australis* (Cav.) ex. Trin. Steud.) habitat tray comprised 21 vertical, living reed stems, randomly distributed over the tray bottom with their intact roots underneath. In each tray, the stem density of 175 stems m^{-2} corresponded to the mean reed density observed in 30 north-east German lakes (Brauns, unpubl. data). The root habitat tray contained a bunch of willow roots of about 120 cm^3, fixed in the tray by a stick. The sand habitat tray simply consisted of the 2 cm layer of sand. The stone habitat tray contained six angular basaltic stones of about 60 cm^3 each, and spaced at 5 cm distances.

The habitat trays each had a comparable surface area of 0.115 m^2. The structural complexity of the five habitats was quantified by their fractal dimension (FD). FD represents habitat complexity across all spatial scales, from surface roughness of single habitat elements to distances between these elements, of the five habitats arranged in the habitat tray. In this sense, structural complexity of the habitat at high resolution levels, like for example roughness of the stones or CWD surfaces could not be captured separately. However, although structural complexity at such high resolution level also influences the ability of invertebrates to withstand wave action (i.e. by providing anchorage points), none of the invertebrate species used in the experiments exhibited a body size matching the size of habitat surface crevices, so that they could have used them to fully escape from waves. FD was calculated following Frontier's grid method (Frontier 1987) on size-comparable top-view digital pictures of the habitat trays. The frame of the habitat tray was taken as the first square of the grid, which was progressively split into finer grids until reaching a level of 4096

squares. The structural complexity of the five habitats increased in the sequence sand (FD=1), CWD (FD=1.29), stones (FD=1.34), reeds (FD=1.39) and tree roots (FD=1.80).

The reduction of wave kinetic energy when the wave was passing through the habitats was quantified as the difference in shear stress in front of and behind the habitat tray. Ten replicated waves were produced for four different levels of shear stress, i.e. 0.43, 1.37, 1.64 and 2.19 N m^{-2}. Differences in shear stress values calculated in front and behind the habitat tray were tested using paired t-tests, and between-habitat differences using ANOVA with associated post hoc test (Scheffé procedure).

Invertebrate species

Five epibenthic invertebrate species (*Bithynia tentaculata* L. [Gastropoda], *Calopteryx splendens* Harris [Odonata], *Dikerogammarus villosus* Sowinsky [Crustacea], *Gammarus roeseli* Gervais [Crustacea] and *Laccophilus hyalinus* DeGeer [Coleoptera]), which are all common in the littoral habitats of German lowland lakes, were used for the experiments. All these species occur in the tested habitats, although *B. tentaculata* and *D. villosus* are eurytopic, *C. splendens* is more abundant in CWD, reed and tree roots, *G. roeseli* generally occurs in tree roots and CWD, and *L. hyalinus* is mainly found in tree roots as well as between stones.

Moreover, these species were selected because they differ considerably in body shape, locomotion behaviour and attachment strategies, all of which should influence their sensitivity to wave impact. Thus, conically shaped *B. tentaculata* attaches by its foot. *Calopteryx splendens* has an elongated body and long legs bearing strong claws, which allow it to firmly grip a wide range of habitat types. *Dikerogammarus villosus* and *G. roeseli* are laterally compressed organisms and actively swim lying on their side, reducing their exposure to flow. *Dikerogammarus villosus* is also known to fix itself strongly in crevices with its two anterior large claws. *Laccophilus hyalinus* exhibits an oval outline and is a highly mobile organism.

B. tentaculata, *C. splendens, G. roeseli* and *L. hyalinus* were collected in the River Spree upstream of Berlin, and *D. villosus* in Lake Müggelsee (Berlin, Germany). New individuals were taken for each experimental series using one of the habitats, in order to avoid individual adaptation to disturbance, or decreasing fitness of individuals. For better visibility on the videos, only large specimens were used (mean body length ± SE, n = 100 for each species: *B. tentaculata* 9.4 ± 0.07 mm, *C. splendens* 15.8 ± 0.3 mm, *D. villosus* 15.3 ± 0.2 mm, *G. roeseli*

13.9 ± 0.1 mm, *L. hyalinus* 4.8 ± 0.04 mm). Individuals were kept in oxygen-saturated water in separate aquaria and fed with appropriate food when not used for experiments.

Experimental design

Experiments followed a crossed design with the five habitats and the five invertebrate species. After 12 h adaptation to habitat conditions in the wave tank, 20 individuals were exposed to single waves of increasing shear stress for each habitat-species combination. The corresponding invertebrate density of 71 ind. m^{-2} represents the lower end of the density range observed in north-east German lakes (Brauns and Leszinski, unpubl. data), so that no artefacts in the responses of the species to hydraulic disturbance could be generated due to strong competition for living space. During the adaptation period, water was oxygenated and the habitat trays were caged in order to prevent dispersal of the individuals. Cages were removed shortly before each single wave was produced and replaced immediately after. Three replicated single waves per shear stress level were produced, with a time interval of 15 minutes, which allowed the individuals that had been detached by the previous wave to fix or hide themselves again. Since each of the three replicated waves corresponded to a distinct experiment and no consistent trend towards increasing or decreasing detachments comparing the three replicates was detected, the numbers of detached individuals resulting from each single wave were used as replicates.

For each wave produced, wave velocity and wave amplitude were recorded to calculate the bottom shear stress. After each wave, the top and side video records were analysed to count the number of individuals detached from the habitat. The shear stress was increased until 100% of the individuals were detached or the maximum applicable shear stress was reached. Mean number of detached individuals for each habitat-species combination, in the following referred to as detachment, was calculated as the overall number of detached individuals divided by the total number of generated waves.

Statistical analysis

Relationships between the proportion of detached individuals and shear stress were explained using sigmoid regression analysis ($\ln y = b_0 + b_1/t$). The sigmoid curve best fitted the observed response of the individuals to hydraulic disturbance since there is a critical shear stress threshold at the lower end of the curve at which individuals started to become detached.

Detachments averaged for the five species studied were compared among habitats using an ANOVA with associated post hoc test (Scheffé procedure). In order to determine the extent to which the selection of species for the study influenced the detachment observed in specific habitats, the proportions of variance explained by species and habitats were calculated separately using multiple classification analysis (MCA, Andrews et al. 1973). MCA is a parametric statistical technique for examining the interrelationship between several predictor variables and one dependent variable in the context of an additive model. It provides the part of explained variance by each predictor, both before and after taking the effects of all other predictors into account. The predictor with the higher explained variance has the greater influence on the dependent variable.

Relationships between the structural complexity of the habitats (expressed by their FD) and the detachment were explored using Spearman rank correlations. Similarly, Spearman rank correlations were also used to explore relationships between structural complexity of the habitats with habitat-specific reduction of shear stress. Deviation of the data from normality and homogeneity of variances were tested using Shapiro-Wilk and Levenè tests before statistical analyses. All statistical tests and regressions were performed using SPSS (v. 9.0, SPSS Inc., Chicago, IL, U.S.A.).

2.3 Results

Impact of wave-induced disturbance on benthic invertebrates

The five species exposed to waves showed a similar response to increasing shear stress in four (sand, coarse woody debris, stones and reeds) of the five habitats studied. In these four habitats, the number of detached individuals generally increased with increasing shear stress (Fig. 4).

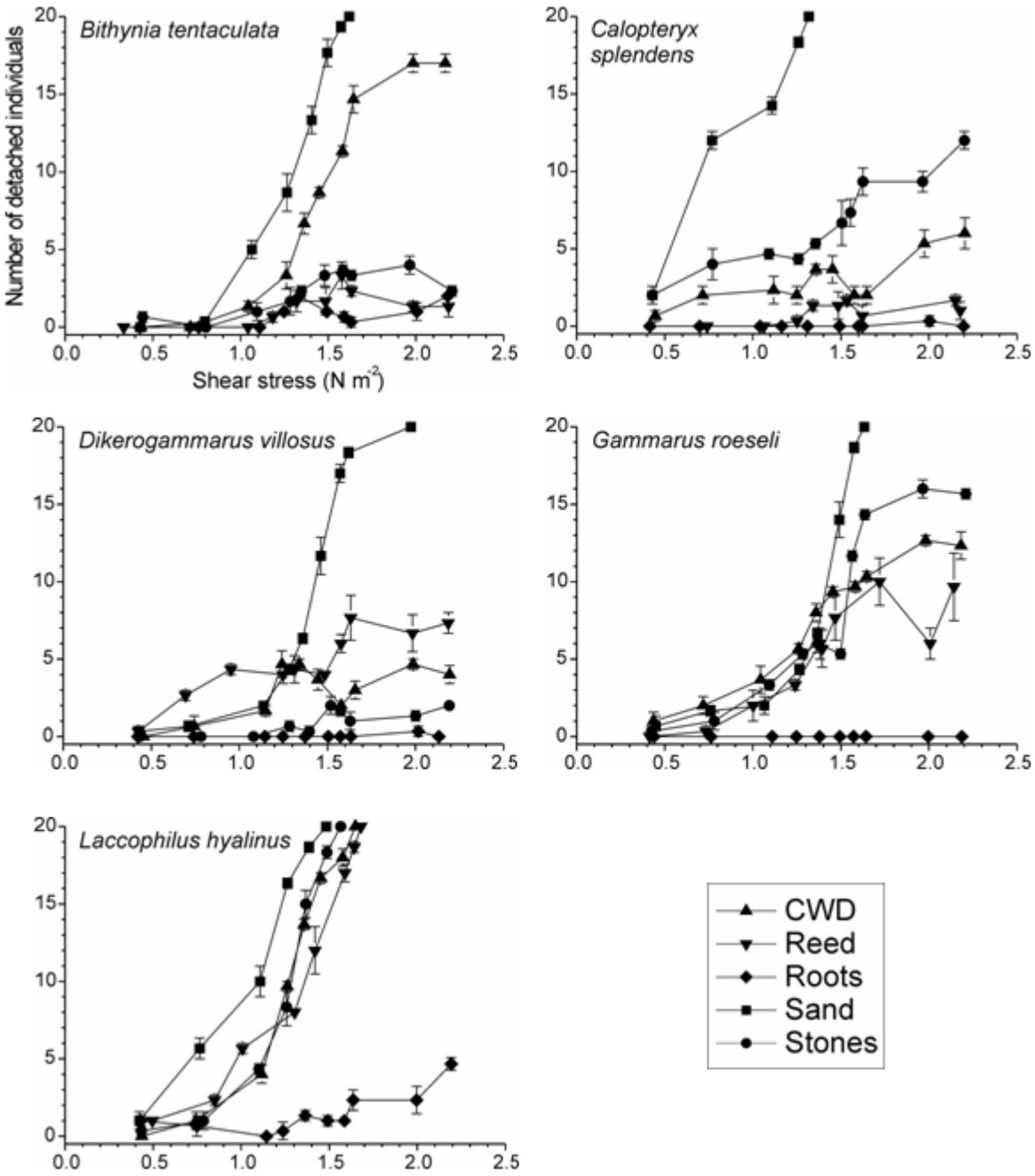

Figure 4: Number of detached individuals from a maximum possible 20 in each habitat for the five species studied as a function of the shear stress caused by experimental waves. Plotted values represent the mean number of detached individuals (± SE) for three replicated waves. Results for each habitat are connected by lines. CWD: coarse woody debris.

These disturbance-response relationships could be well described by sigmoid regression models (Table 4), except for *B. tentaculata* on stones, where the relationship was not significant ($P > 0.05$). Conversely, such a pattern was not observed in tree root habitat where only a few individuals of each species were detached even by the strongest waves (Fig. 4). Here, a significant regression ($R^2 = 0.52$, $P = 0.01$) could only be found for *B. tentaculata*.

Table 4: Sigmoid regression analysis ($\ln y = b_0+b_1/t$) between number of detached individuals and shear stress. For each test, the R^2 value (adjusted for degrees of freedom), the corresponding significance levels (*** $p<0.001$, ** $p<0.01$, * $p<0.05$, n.s. not significant) and the curve coefficients (b_0 / b_1) are given (CWD = coarse woody debris).

	CWD	Reeds	Roots	Sand	Stones
Bithynia tentaculata	0.81*** (7.9 / -94.0)	0.48* (2.4 / -56.3)	0.52* (3.3 / -75.3)	0.96*** (8.0 / -80.1)	0.02 n.s. (1.8 / -26.0)
Calopteryx splendens	0.66* (1.8 / -9.7)	0.64* (9.2 / -157.8)	0.05 n.s. (-9.1 / -14.3)	0.94*** (3.8 / -12.5)	0.79*** (2.5 / -8.5)
Dikerogammarus villosus	0.84*** (6.1 / -71.3)	0.92*** (2.8 / -15.3)	0.06 n.s. (-9.2 / -14.4)	0.81*** (3.8 / -24.0)	0.56** (3.7 / -80.2)
Gammarus roeseli	0.92*** (3.1 / -14.8)	0.94*** (6.6 / -70.0)	0	0.77** (3.7 / -21.0)	0.88*** (3.5 / -21.3)
Laccophilus hyalinus	0.92*** (8.0 / -78.6)	0.91*** (4.0 / -21.5)	0.12 n.s. (-0.5 / -5.0)	0.98*** (4.0 / -16.7)	0.88*** (4.2 / -25.0)

Role of habitat structural complexity

Detachments averaged for the five species (mean ± SE) varied among habitats. More individuals were detached on sand (20 ± 0) than on CWD (11.9 ± 1.7), stones (10.4 ± 1.9), reeds (7.9 ± 1.9) and tree roots (1.3 ± 0.5). The detachments were significantly higher (ANOVA, Scheffé post hoc test, n = 75) on sand than on all other habitats ($P < 0.001$, n = 75), and significantly lower on tree roots than on all other habitats ($P = 0.022$ at the lowest, n = 75). Conversely, no significant differences in detachments were observed between CWD, stones and reeds ($P > 0.05$, n = 75).

Comparison of the detachments of each species showed species-specific responses to wave-induced hydraulic disturbance according to habitats (Table 4). On CWD, more individuals of *B. tentaculata*, *G. roeseli* and *L. hyalinus* were detached than individuals of *C. splendens* and *D. villosus*. On reed, more individuals of *D. villosus*, *G. roeseli* and especially *L. hyalinus* were detached than individuals of *B. tentaculata* and *C. splendens*. On stones, more individuals of *C. splendens*, *G. roeseli* and *L. hyalinus* were detached than individuals of *B. tentaculata* and *D. villosus*. Even on sand and tree root habitats, differences in detachments among species were recorded (Table 5).

Table 5: Mean number of detached individuals (average across replicates ± SE, n = 3) for the cross combinations of species and habitats studied (CWD = coarse woody debris).

	CWD	**Reeds**	**Roots**	**Sand**	**Stones**
Bithynia tentaculata	8 ± 0.2	1.23 ± 0.0	1.47 ± 0.1	10.54 ± 0.4	2.23 ± 0.1
Calopteryx splendens	2.97 ± 0.1	0.8 ± 2.1	0.03± 0.0	13.27 ± 0.3	6.5 ± 0.3
Dikerogammarus villosus	2.9 ± 0.1	4.73 ± 0.1	0.03 ± 0.0	8.96 ± 0.2	0.9 ± 0.1
Gammarus roeseli	7.47 ± 0.1	5.07 ± 0.5	0.0 ± 0.0	8.5 ± 0.3	7.9 ± 0.2
Laccophilus hyalinus	10.54 ± 0.2	10.58 ± 0.3	1.47 ± 0.1	11.94 ± 0.3	9.62 ± 0.3

To determine the extent to which these species-specific responses might influence observed differences in the detachments among habitats, we conducted a Multiple Classification Analysis (MCA). Results showed that 77% of the variance in detachments was explained by habitat type (value corrected from the influence of the species factor) versus 47% by species (value corrected from the influence of the habitat factor - full model: r^2=0.81, p<0.001, N=75). Hence, the choice of the five species did not compromise the conclusion that the habitat had the strongest influence on detachment in wave experiments.

The impact of the wave-induced hydraulic disturbance on invertebrates was found to decrease along the gradient of habitat structural complexity parameterised by the fractal dimension (Fig. 5A). Detachments averaged for the five species were significantly negatively correlated to the fractal dimension of the habitats (Spearman's Rho = -0.99, $P < 0.001$, n = 5). Considering each species separately, significant negative correlations were found for *B. tentaculata* (Spearman's Rho = -0.99, $P < 0.001$), *C. splendens* (Rho = -0.90, $P < 0.05$), and *G. roeseli* (Rho = -0.90, $P < 0.05$).

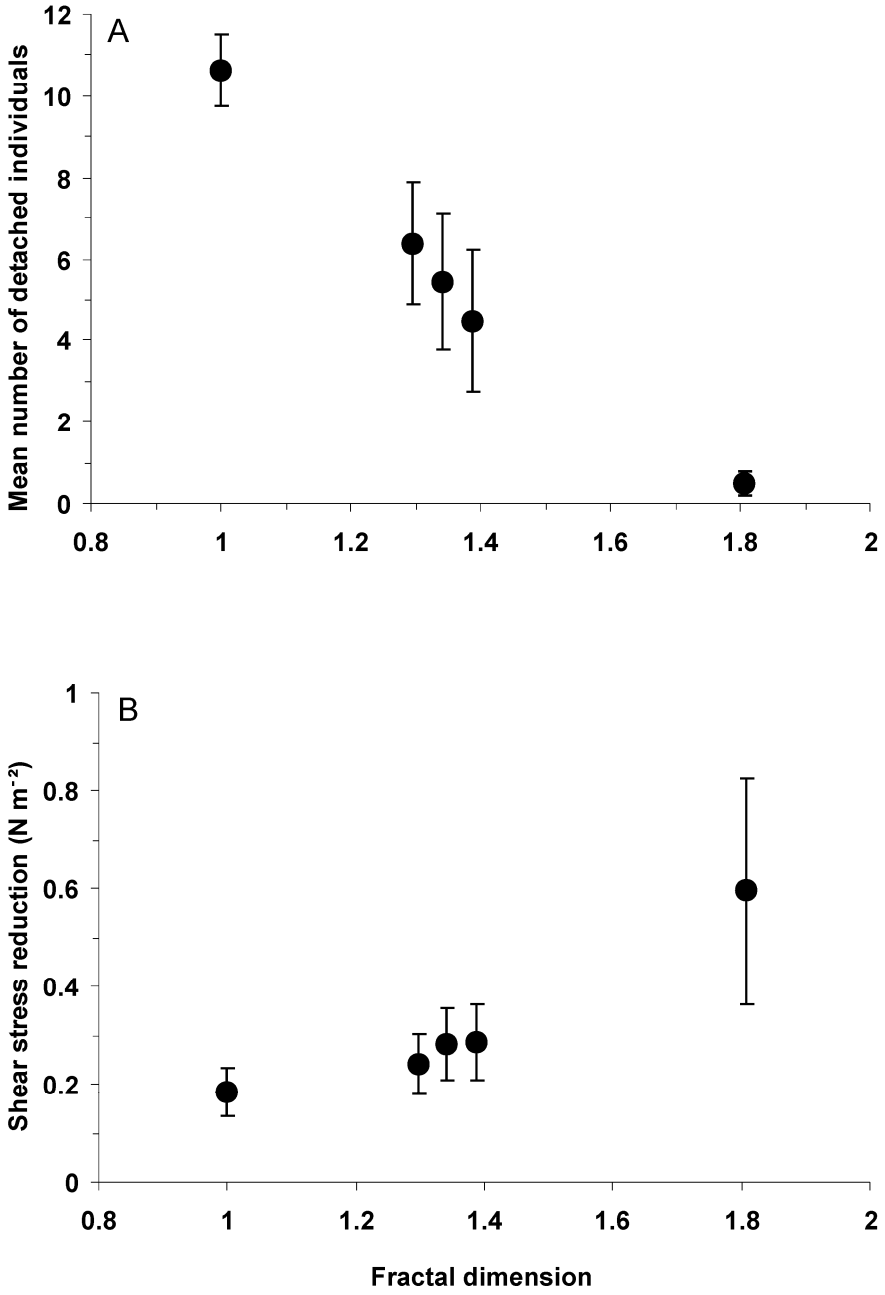

Figure 5: Relationships to the fractal dimension of the habitats of (A) the mean number (average for the five species ± SE, n = 15) of detached individuals, and (B) the shear stress reduction (mean ± SE for four initial shear stress levels: 0.43, 1.37, 1.64 and 2.19 N m^{-2}, n = 10 each) caused by the habitats.

Shear stress in front of and behind the habitat

Shear stress measured in front of and behind the habitat trays differed significantly for all habitats ($P < 0.001$ for all tests, n = 10 per test). Shear stress reduction tended to increase in the sequence: sand, CWD, stones, reeds and tree roots (Fig. 6). Only waves of low initial shear stress (0.43 N m^{-2}) showed no significant differences in reduction of shear stress among habitats ($P > 0.05$, n = 50). For stronger waves (1.37, 1.64 and 2.19 N m^{-2}), shear stress

reduction was significantly different between sand and stones (P = 0.014 at the lowest, n = 50), sand and reed (P = 0.001 at the lowest, n = 50) except for waves of 1.37 N m^{-2}, as well as between roots and the other habitats (P = 0.012 at the lowest, n = 50). No significant differences were recorded between CWD, stones and reed habitats, except for waves of 2.19 N m^{-2}, where shear stress reduction in stones was significantly higher (P < 0.001, n = 50) than in CWD (Fig. 6). The reduction of shear stress caused by the habitat was correlated with the structural complexity of the habitat (Fig. 5B), as shown by the significant positive correlations found between habitat-specific shear stress reductions and habitat fractal dimensions for three of the four shear stress levels tested (1.37 N m^{-2}: Spearman's Rho = 0.90, P < 0.05; 1.64 and 2.19 N m^{-2}: both Rho = 0.99, P < 0.001).

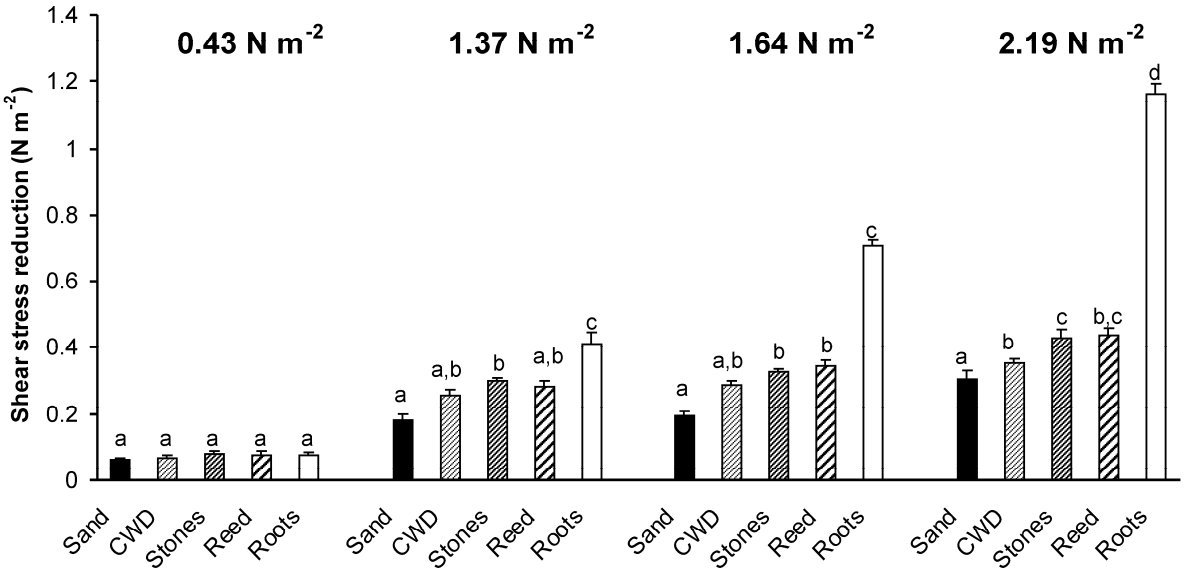

Figure 6: Reduction of shear stress (mean ± SE, n = 10 each) caused by the five habitats studied under the four different shear stress levels indicated. Shear stress reduction was calculated as the difference between shear stress values measured in front of and behind the habitat tray. Bars with different letters indicate significant differences among habitats for a given shear stress level (ANOVA, Scheffé post hoc test, n = 50). CWD: coarse woody debris.

2.4 Discussion

Impact of wave-induced hydraulic disturbance on benthic invertebrates

In our experiments, clear relationships were found between wave-induced shear stress and invertebrate detachment for all habitats except roots, and for each species studied. Our observations were best described by a sigmoid regression model, which revealed a threshold of shear stress corresponding to the beginning of mass detachment of invertebrates. This threshold varied according to the habitat-species combination considered, but was mainly observed to be at 1.0-1.2 N m^{-2}. Furthermore, 50% of individuals were already detached at

shear stress values from 1.5 N m^{-2}. Such shear stress values were produced in the wave tank by waves with an orbital velocity of 19 to 42 cm s^{-1}, and bottom shear stresses produced under natural conditions by boats are generally higher. For example, maximum orbital velocities measured in the littoral zones of Lake Langer See and the River Spree ranged from 21 to 44 cm s^{-1} for small private boats, up to 54 cm s^{-1} for freight barges and up to 65 cm s^{-1} for passenger ships (D. Franke, unpubl. data), which indicates that hydraulic disturbance created in the wave tank corresponded to the lowest disturbance experienced by benthic invertebrates in natural conditions. Moreover, due to their large dimensions, passenger ships or commercial barges create waves that tend to break before they reach the shoreline. Such breaking waves produce even more severe hydraulic conditions and the detachment of invertebrates is likely to be higher under those conditions than in the wave tank. Hence, detachment of invertebrates by waves should also occur under field conditions and is probably a widespread phenomenon in the littoral zones of navigable waterways.

Complex habitats provide refuge for invertebrates

The detachment of invertebrates by wave-induced hydraulic disturbance was found to be significantly reduced in complex habitats that provide numerous refuges and anchorage points enabling individuals to resist drag forces imposed by peaks in flow velocity. Sand did not offer suitable hiding or fixing options for any of the five species and as a result, mass detachment of individuals started here at low stress values (0.4-0.8 N m^{-2}). In contrast, root habitats offered maximal sheltering conditions for all the studied species, and the dense network of tiny, flexible branches of the root network allowed every species, irrespective of its size or gripping abilities, to enter the network and fix itself. Even *B. tentaculata*, for which the tiny root branches do not offer optimal surfaces for efficient foot adhesion, showed a low detachment here.

Slightly fewer individuals were detached in reed than in stones or coarse woody debris (CWD) habitats. However, since no significant differences were recorded between these three habitats in the detachments of all five species combined, these habitats evidently offered a similar level of protection against detachment despite their differing fractal dimensions. Nevertheless, the five species showed differences in detachments among these three habitats, and species-specific differences in detachments were also observed for a given habitat. Furthermore, significant negative correlations between detachment and habitat fractal dimension were found for only three of the five species studied. Thus, detachment did not only depend on habitat complexity, but also partially on the extent to which species-specific

fixing or hiding capabilities matched the physical habitat characteristics. For example, the rough ridges of CWD provided good anchorage points for species fixing themselves with big claws, such as *C. splendens* and *D. villosus*, but not for either *B. tentaculata*, which needs smoother surfaces for efficient attachment, or for *G. roeseli* and *L. hyalinus*, which possess smaller claws. Similarly, reeds provided better sheltering conditions against waves for *B. tentaculata* and *C. splendens* than for *L. hyalinus* and the two crustaceans. Reed stems provided an ideal smooth surface for *B. tentaculata*, while *C. splendens* was able to fix itself by gripping the reed stems between its long legs. In contrast, the claws and legs of *L. hyalinus, D. villosus* and *G. roeseli* were far too small to grip reed stems firmly. Species such as *L. hyalinus* and *G. roeseli*, which do not exhibit morphological or behavioural characteristics matching the structural characteristics of the CWD, stone or reed habitats used in the experimental wave tank, were strongly detached.

Despite specific habitat-species relationships, the structural complexity of the habitat has proved to influence the degree of protection of benthic invertebrates against wave-induced hydraulic disturbance. The higher proportion of variance in detachments explained by habitat features alone, in comparison to the influence of the species used, supports the conclusion that there is a strong causal relationship between detachment and the structural complexity of the habitat. Comparable influences of habitat complexity in sheltering benthic invertebrates against hydraulic disturbance have been demonstrated for *Seratella ignita* and *Gammarus pulex* exposed to high currents (Borchardt 1993). In that study, the proportion of drifting individuals decreased as more and more woody debris was added to the sandy bottom of a circular flume. *Seratella ignita* started to drift at lower shear stress values (1.1 N m^{-2}) than *G. pulex* (3.1 N m^{-2}), a fact attributed to behavioural differences between the swiftly swimming *G. pulex* and the slowly crawling *S. ignita*.

Habitat complexity dissipates wave kinetic energy

Besides providing refuges for the organisms, the spatial structure of benthic habitats also influences the hydrodynamics in their surroundings (Grass 1971). From the perspective of flow mechanics, the structure of the habitat provides obstructions to the unidirectional flow, transforming some portion of the mean flow into turbulent components. In turbulent flows, the kinetic energy is extracted by larger vortices from the mean flow, transferred by the cascade of turbulences towards smaller scales, where it finally dissipates into heat due to molecular viscosity (Tennekes and Lumley 1972; Townsend 1976). Correspondingly, higher structural complexity provides more obstacles to flow and dissipates a larger portion of

kinetic energy. Notably, with almost 1.2 N m^{-2} of shear stress reduction, which corresponds to 54% of the shear stress caused by the strongest wave produced in the wave tank, roots were three to four times more efficient in dissipating kinetic energy than any other habitat studied. A direct implication for invertebrates is that in more complex habitats, hydraulic disturbance is attenuated after a short distance inside the habitat patch, so that even small patches of complex habitat may serve as effective refuges.

On the other hand, generated turbulences may potentially increase detachment of individuals since the erratic flow pattern creates drag forces constantly varying in direction. Shear-stress distribution depends on the spatial arrangement of the habitat elements providing obstacles to flow and is even more complex in presence of turbulences, so that the relative influences of refuges, dissipation of wave kinetic energy or turbulences on invertebrate detachment are difficult to assess separately. As a general pattern, habitat efficiency to dissipate wave energy was found to increase following the habitat sequence CWD, stones and reeds. In parallel, for species whose specific fixing capabilities do not strongly match fixing options of a specific habitat (i.e. *C. splendens* and reeds), intensity of detachment was found to follow a reverse habitat sequence. For example, *C. splendens* and *G. roeseli* were more detached in stone habitat than in CWD habitat. Similarly, *D. villosus* was more detached in reed habitat than in CWD or stone habitats. Hence, it is likely that refuges provided by complex habitats as well as how habitat structure matches species fixing capabilities, act as the main factor in sheltering invertebrates. Concomitantly, in more complex habitats, waves are attenuated after a shorter distance, improving sheltering conditions for invertebrates.

Implication for shoreline management

We could show that the effect of wave disturbance resulted in significant detachment of invertebrates even at moderate shear stress levels. Since ship-induced waves occur stochastically and create harsh hydraulic conditions, they constitute a major hydraulic disturbance for invertebrates inhabiting shoreline habitats. The threshold values at which invertebrates started to be detached were lowest in the sand habitat (0.4-0.8 N m^{-2}), intermediate in the other habitats (1.4-1.6 N m^{-2}) and not reached for roots even at the maximum shear stress levels produced in the wave tank (2.19 N m^{-2}). It can be concluded that network habitats such as tree roots, and to a certain extent also dense reed belts, provide efficient protection of invertebrates against wave-induced disturbance. Mechanistic explanations are that complex three-dimensional habitats provide both the best options for all species to hide or to fix themselves, and also the strongest dissipation of kinetic wave energy.

Consequently, complex habitats such as tree roots and dense reed belts should be protected to preserve a diverse and natural fauna in the littoral zone of inland waterways, as required by water policies. These habitats are often removed during shoreline stabilisation, which in urban areas results in two additive constraints on the littoral fauna, i.e. simplification of habitat structure and increase of hydraulic stress. Also, tree root habitats and reed stands may be heavily damaged if ship-induced waves occur repeatedly over the long-term (Ostendorp 1989, 1999), amplifying the short-term ecological effects of ships passing by. These factors lead to a reduction in species richness and decreased abundances of the benthic communities (Bishop 2003, 2004, 2005) in wash-zones. Thus, water managers should be able to reduce ship-induced disturbance in the littoral zone to a level lower than the detachment threshold for typical species, so that invertebrate assemblages in wash-zones maintain similar structure and abundance patterns as in non-wash zones.

Acknowledgements

The authors wish to thank R. Biskupek for his technical help in constructing the wave tank, T. Hintze and W. Sauer for their help in installing and calibrating the electronic devices, C. Wagner and S. Wilhelm for helpful discussions about statistical tests, as well as R. Lehmitz and J. Höhle for their informal help in running the experiments. We are indebted to H. Bungartz for his advice regarding hydrodynamics.

3 Effects of ship-induced waves on benthic invertebrates in navigable surface waters

Friederike Gabel, Xavier-François Garcia, Ingo Schnauder and Martin T. Pusch

(under review at *Journal of Applied Ecology*)

Abstract

1. It has been shown that ship-induced waves can affect the physical characteristics of lake and river shorelines, and significant effects on littoral invertebrates have been suspected based on laboratory results. In this study, we explored if these effects could be directly observed under field conditions on a natural lake shore affected by wave sequences (trains) produced by boats.

2. Individuals of five invertebrate species (*Bithynia tentaculata*, *Calopteryx splendens*, *Dikerogammarus villosus*, *Gammarus roeselii*, *Laccophilus hyalinus*) were exposed to waves with increasing shear stress in five habitats differing in their structural complexity.

3. Detachment of invertebrates rose with increasing shear stress, following sigmoid response curves. Detachment of invertebrates was mitigated by the structural complexity of the habitats, and detachment rate was influenced more by habitat type than by species. To leave 90% of the individual invertebrates unaffected, the threshold stress level is 0.64 N m^{-2} in a structurally-complex reed habitat, but 0.37 N m^{-2} in a simple sand habitat.

4. Shear stress associated with the wave trains created by typical recreational boating at a distance of 35 m from the shore at 11 km h^{-1} lead to the detachment of 45% of littoral invertebrates. Decreasing the boat to shore distance to 20 m increased wave shear stresses by 30% and invertebrate detachments up to 75%.

5. *Synthesis and applications*. Disturbance of littoral invertebrates is a significant and wide-spread anthropogenic impact to aquatic ecosystems in inland waters used for recreational or commercial navigation, but which has been mostly neglected so far. Persistent alterations in the structure of littoral benthic invertebrate assemblages will appear in case complex littoral habitats have disappeared due to shoreline development, or due to repeated

hydraulic disturbance by ship-induced waves. Hence, we expect that the integrity of littoral zones of navigable surface waters could be much improved by implementing management measures aiming to decrease wave disturbance of invertebrates by physically protecting complex habitats such as dense reed belts and tree roots, or reduced speeds for watercraft and/or minimum distances from shorelines.

3.1 Introduction

Littoral zones of lakes and rivers are among the most productive, but most threatened, aquatic habitats in the world (Vadeboncoeur et al. 2001; Jenkins 2003; Strayer and Findlay 2010). Being characterized by a complex spatial structure and associated gradient of environmental conditions, littoral zones provide habitats for numerous species of water fowl, fish and invertebrates (Strayer and Findlay 2010). However, littoral zones are often heavily modified, as they are preferred for human settlement and intensively used for recreation (Gonzalez-Abraham et al. 2007). Activities affecting littoral areas include angling and swimming as well as boating and inland navigation (see reviews of Liddle and Scorgie 1980; Burgin and Hardiman 2011). Mechanic damage by boats, pollution and the mechanical impacts from ship-induced waves may cause significant disturbances to littoral flora and fauna (Mosisch and Arthington 1998). The intensity of wave-induced disturbance depends on vessel characteristics such as travelling speed, draught and distance to shoreline. Characteristics of the water body and shoreline that can influence the impacts to littoral zones include water depth, slope and width of the water body. Ship-induced waves increase shoreline erosion, sediment suspension and turbidity (Hilton and Phillips 1982; Garrad and Hey 1987; deWit and Kranenburg 1997; Anthony and Downing 2003) and may even uproot and negatively affect growth of aquatic macrophytes (e.g. Liddle and Scorgie 1980; Murphy and Eaton 1983; Asplund and Cook 1997). Intense wave action may also displace juvenile fish (e.g. Morgan et al. 1976; Holland 1986; Arlinghaus et al. 2002; Wolter and Arlinghaus 2003; Wolter et al. 2004; Kucera-Hirzinger et al. 2009), affect fish feeding behaviour (Stoll and Fischer 2011), and alter predator-prey relationships between fish and invertebrates (Gabel et al. 2011b).

Recent studies have suggested that ship-induced waves will also affect aquatic invertebrates colonizing littoral zones, thus impacting a key element of the food web. Bishop (2008) found that waves generated by a small vessel may detach invertebrates from flapping seagrass blades in a coastal Australian lagoon, thereby reducing abundance and species richness for at least one hour after the disturbance.

In experiments conducted in a laboratory flume using various substrates mimicking typical littoral habitats, the number of detached invertebrates increased with higher wave induced shear stress (Gabel et al. 2008b), following a sigmoid-shaped response pattern. The detachment rate was significantly lower in structurally-complex habitats, such as reed and submerged tree roots, since they offer better fixing possibilities for invertebrates, and also dissipate the kinetic energy of waves more efficiently. Conversely, habitats with low structural complexity, such as sand, provide little fixing possibilities for invertebrates and are less effective at dissipating wave kinetic energy (e.g. Knutson et al. 1982; Gabel et al. 2008b). In these various laboratory experiments both the detaching effect on invertebrates and its mitigation by habitat structure were substantial. Although laboratory investigations have provided evidence for a significant wave effect on invertebrates, field studies are needed to confirm the laboratory results. Waves created under laboratory conditions in a wave tank were solitary waves (solitons). Water craft, on the other hand, generate wave trains, that is, a series of several waves striking an area in rapid sequence. The impact of the latter may differ substantially from the former.

We conducted a series of measurements in the near-natural littoral zone of a lake in order to quantify the effects of ship-induced waves. The goal of this study was to evaluate, under real-world conditions, the relationship between wave-induced shear stress, habitat complexity and the number of detached individuals. Individuals of the same five species used in previous laboratory studies were exposed on patches of the same five habitats (coarse woody debris, reed, sand, stones and tree roots) to ship-induced waves, with shear stresses ranging from 0.3 to 1.5 N m^{-2} (0.4 to 2.2 N m^{-2} under laboratory conditions).

3.2 Material and Methods

Experimental set up

Experiments were conducted along the shore of Lake Kalksee located south-east of Berlin (52°27’30’’ N, 13°6’9’’ E) in September 2007. Lake surface area is 84 ha (2 km length and 650 m width at maximum) with a maximum water depth of 10 m. Lake Kalksee is connected to the River Spree and used as a navigational waterway for barges and recreational boats. Ship traffic is nevertheless low. The study site was located on an open, gently-sloping sandy beach on the eastern shore. Water in that area generally has low turbidity. Water temperature during the experiment was 13°C with a pH of 8.5, a conductivity of 1300 µS cm^{-1} and a daily-average dissolved oxygen concentration of 8 mg l^{-1}. Experiments were conducted at a water

depth of 25-30 cm. Experimental set up consisted of three replicate cages (140 x 60 x 50 cm; L x W x H) that were open at the top, bottom and front. The remaining three sides were covered by 1 mm nylon mesh (Fig. 7). In each cage, smaller, solid-wall Perspex cages (60 x 34 x 40 cm) were placed to prevent the escape of invertebrate test organisms between the experimental runs, when no waves were created. The smaller Perspex cages were removed before a wave hit the study area, whereas the larger net cages were left in place in order to prevent invertebrates from being displaced too far. Five different habitats were installed in the Perspex cage which served as the substratum for specimens representing five different invertebrate species that were subsequently exposed to ship-induced waves.

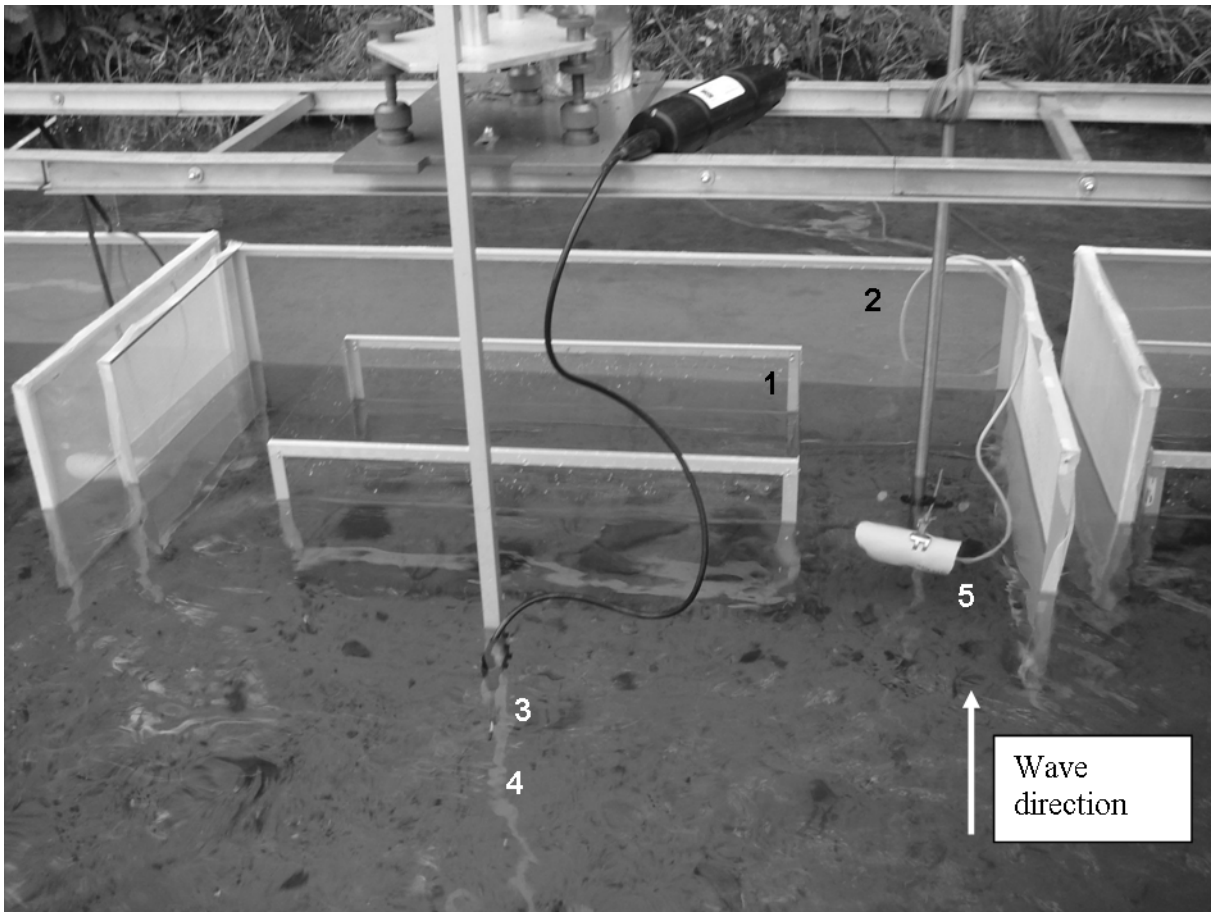

Figure 7: Experimental set up on the lake shore. Removable Perspex cage (1), in which invertebrates were exposed in different habitats (here stones). Fixed cages (2) surrounding the Perspex cage. Vectrinos (3) and pressure sensors (4) used to measure wave characteristics. Under-water video cameras (5) used to record invertebrate detachment.

Wave velocity was measured with three Vectrinos (recording at 25 Hz; Nortek AS, Rud, Norway), placed in a central position 25 cm in front of the habitats being measured, 5 cm above the ground. Wave heights were recorded by three pressure sensors (CAU-T precision pressure transmitters 2nd generation, 10 Hz, Aktiv Sensor, Stahnsdorf, Germany) buried in the sand underneath the Vectrinos so that only about 0.5 cm of the pressure transducer was visible

above the sand. Each study area was surveyed by an underwater camera (Selvac OC-1, Selvac, Leer, Germany) placed next to the habitats in order to determine the number of detached individuals.

Waves were generated with a 6.5 m long, V-hulled vessel having a width of 2.3 m, a displacement of 1 m³ and a motor capacity of 36.8 kW. The vessel passed the study site at varying speeds and distances from shore. Vessel velocity was determined by GPS (nüvi 550 Garmin, Olathe, KS, USA) and distance to shore was measured with a Laser Golf Rangefinder (Nikon, Düsseldorf, Germany).

Habitats

Five habitats (Coarse Woody Debris [CWD], reed, sand, stones and tree roots), each covering an area of 0.23 m², were placed subsequently in the Perspex cages. These habitats exhibited contrasting structural complexity and were spatially arranged as in previous laboratory experiments (Gabel et al. 2008b). The CWD habitat was comprised of four flat pieces of ridged bark. Reed habitat consisted of 42 reed (*Phragmites australis* (Cav.) ex. Trin. Steud.) stems randomly distributed in the cages resulting in a density of 175 stems m^{-2}. The sand habitat consisted of the local bottom sediment (d_{50}=0.7 mm). The stone habitat was comprised of 12 basaltic stones of about 60 cm^3 each, oriented randomly and spaced 5 cm apart. The tree root habitat contained two bunches of willow roots, each fixed in the sand by a stick. Habitat structural complexity was quantified by the fractal dimension (FD) of the habitat, calculated using top view photos following the Frontier's grid method (Frontier 1987). Sand had the lowest structural complexity (FD=1), followed by CWD (FD=1.30), stones (FD=1.36) and reed (FD= 1.42). Tree roots had the highest structural complexity (FD=1.81). The FDs of the habitats used for field validation were comparable to those of the habitats used in the previous wave flume experiments (sand: FD = 1, CWD: FD = 1.29, stones: FD = 1.34, reed: FD = 1.39 and tree roots: FD = 1.80; (Gabel et al. 2008b).

Invertebrate test species

Five species, differing in body shape and attachment strategy, were studied. The organisms were comparable in body size to those used for the earlier laboratory experiments (Gabel et al. 2008b). The test species (300 individuals of each) were *Bithynia tentaculata* L. [Gastropoda] (mean body length ± SE, 9.5 ± 0.07 mm), *Calopteryx splendens* Harris

[Odonata] (15.9 ± 0.4 mm), *Dikerogammarus villosus* Sowinsky [Crustacea] (15.2 ± 0.2 mm), *Gammarus roeselii* Gervais [Crustacea] (14.0 ± 0.2 mm) and *Laccophilus hyalinus* DeGeer [Coleoptera] (4.8 ± 0.04 mm). Individuals were collected from the River Spree and Lake Müggelsee (for further details see Gabel et al. 2008b) which are part of the same river system as Lake Kalksee, where studies were conducted. Prior to the experiment, individuals were kept in aerated water from Lake Kalksee. New individuals were taken for each habitat-species combination and each replicate, in order to avoid individual adaptation to disturbance, or decreasing fitness of individuals.

In order to facilitate visual distinction of detached individuals from drifting organic or inorganic particles, individuals were marked with bright colours. Marking methods differed among species. *Calopteryx splendens* and *B. tentaculata* were marked with white nail lacquer containing a small amount of bright orange stamping ink. *Laccophilus hyalinus* individuals received a small dot of the white lacquer on their dorsal surfaces. These colours were easily visible under water. To mark amphipods, a small piece of pink foil was applied to their dorsal surface with superglue. All marking methods were tested several weeks before the start of the experiments using different individuals. No changes in the behaviour or the survival rate of the invertebrates were observed after marking.

Experimental design

Experiments followed a cross-design between the five habitats and the five invertebrate species. Twenty individuals were exposed to waves of increasing shear stress for each replicated habitat-species combination. Waves of six different shear stress levels were generated, with an inter-wave time interval of 15 min. This time period allowed previously-detached individuals to reattach or hide themselves again, and to recover from disturbance. The interval between the experiments reflects conditions in navigable waterways. On the nearby Havel River, for example, the interval of ship passage was determined to be 10.3 ± 2.4 min (unpubl. data). The Perspex cages were removed shortly before each wave was produced and replaced immediately after. For each wave produced, wave velocity and wave amplitude were recorded, and one operator per cage was visually counting individuals that were detached. Additionally, video records were analyzed as a quality control check of the visual counts. Each experiment was replicated three times.

Shear stress calculation and wave characteristics

Maximum shear stress (τ, N m^{-2}) of the wave trains generated by the vessel in front of the habitats was calculated as:

$$\tau = 0.5\rho f_w U_b{}^2 / 10$$

where ρ is the density of water (1 g cm^{-3}), f_w is the wave friction factor and U_b (cm s^{-1}) is the orbital wave velocity. Wave friction factor was calculated following Dyer (1986) as:

$$f_w = 2\sqrt{\frac{\nu}{U_b A_b}}$$

where ν is the kinematic viscosity of water (~0.01 cm^2 s^{-1}) and A_b (cm) is the maximum bottom wave amplitude, since shear stress was mainly produced by main flow, as flow was not turbulent. Reynolds numbers were approximately 10^4, which is one order of magnitude lower than the critical value for turbulent flow (Jensen 1989).

The vessel passed the study area at five different speed levels (9 to 18 km h^{-1}) and two distances to the shoreline (20 and 35 m), creating reproducible waves of six different shear stress levels ranging from 0.3 to 1.5 N m^{-2} (Table 6). Wave trains consisted of several wave crests hitting the study area for 20 to 60 s. For each shear stress level, no significant difference in shear stresses among the three replicates was recorded (ANOVA, n=25 per test, $p>0.05$ for all tests).

Table 6: Characteristics of vessel passages (n=25) and resulting wave parameters (mean ± SD) at the study site.

Vessel speed (km/h)	Distance to shore (m)	Max. wave velocity (cm s^{-1})	Max. wave height (cm)	Max. shear stress (N m^{-2})
9	35	10.51 ± 2.26	3.69 ± 0.94	0.26 ± 0.08
11	35	16.15 ± 3.31	4.84 ± 0.71	0.44 ± 0.09
11	20	21.19 ± 3.58	5.35 ± 0.80	0.63 ± 0.10
12	20	34.67 ± 4.17	9.52 ± 2.01	0.95 ± 0.10
14	20	44.95 ± 5.95	12.96 ± 1.37	1.21 ± 0.13
18	20	55.31 ± 8.78	14.93 ± 1.81	1.51 ± 0.12

Statistical analysis

Sigmoid regression analysis ($\ln y = b_0 + b_1/t$) was used to describe the relationships between the number of detached individuals and bottom shear stress, since a sudden

exponential increase in the number of detached individuals was observed above a certain threshold, which levelled out at high shear stress levels. Average detachments for the five species studied were compared among habitats using analysis of variance (ANOVA) with an associated post hoc test (Scheffé procedure). In order to determine if the observed number of detached individuals among habitats was influenced by the selected species, the proportion of variance respectively explained by species and habitats was calculated separately using a multiple classification analysis (MCA, Andrews et al. 1973; see Gabel et al. 2008b for detailed explanations).

The relationship between the structural complexity of the habitats (expressed as their fractal dimension) and detachment of invertebrates was explored using Spearman rank correlations. In order to compare detachment rates recorded in laboratory flume and field experiments, non-parametric tests for paired samples (Wilcoxon-tests) were used.

Deviation of the data from normality and homogeneity of variances were tested using Shapiro-Wilk's and Levene tests before statistical analyses. All statistical tests and regressions were performed using PASW Statistics (v. 17, SPSS, Chicago, IL, USA.).

3.3 Results

Results of field experiments

In most experiments, the number of detached individuals increased with increasing shear stress (Fig. 8). As an overall estimate, 10% of the individuals were detached at a shear stress of 0.4 N m^{-2}, 25% were detached at a shear stress of 0.6 N m^{-2}, and 50% were detached at a shear stress of 1.2 N m^{-2} (average for all species and for all habitats). For all species in coarse woody debris, reed, sand and stone habitats, significant sigmoid relationships between wave-induced shear stress and number of detached individuals could be established which explained, on average, 72% of the variance. Response curves revealed typical phases, which can be recognized as an initial low-effect phase followed by a steep increase in the detachment effect, and finally a saturation phase (e.g. Fig. 8, *B. tentaculata* in sand). In contrast, this type of relationship was not significant for four out of five of the investigated species in the root habitat (Table 7).

The number of detached individuals (averaged for the five species at the highest level of shear stress) varied among habitats. Significantly more individuals were detached from sand (mean ± SE, 19.9 ± 0.1; p=0.003 at the lowest; ANOVA, Scheffé post hoc test, n = 75) than from CWD (12.3 ± 1.4), stones (11.5 ± 1.9) or reed (10.9 ± 1.6) (no significant differences

among these three) and tree roots (1.1 ± 0.5). Significantly fewer individuals ($p<0.001$) were detached from roots than in all other habitats. In sand, 10% of individuals were detached at an average shear stress of 0.37 N m^{-2}. In reed habitat, 10% detachment of organisms did not occur until the shear stress reached 0.64 N m^{-2} (average for all species). For three species in roots, the detachment level remained below 10% even under the highest shear stress levels.

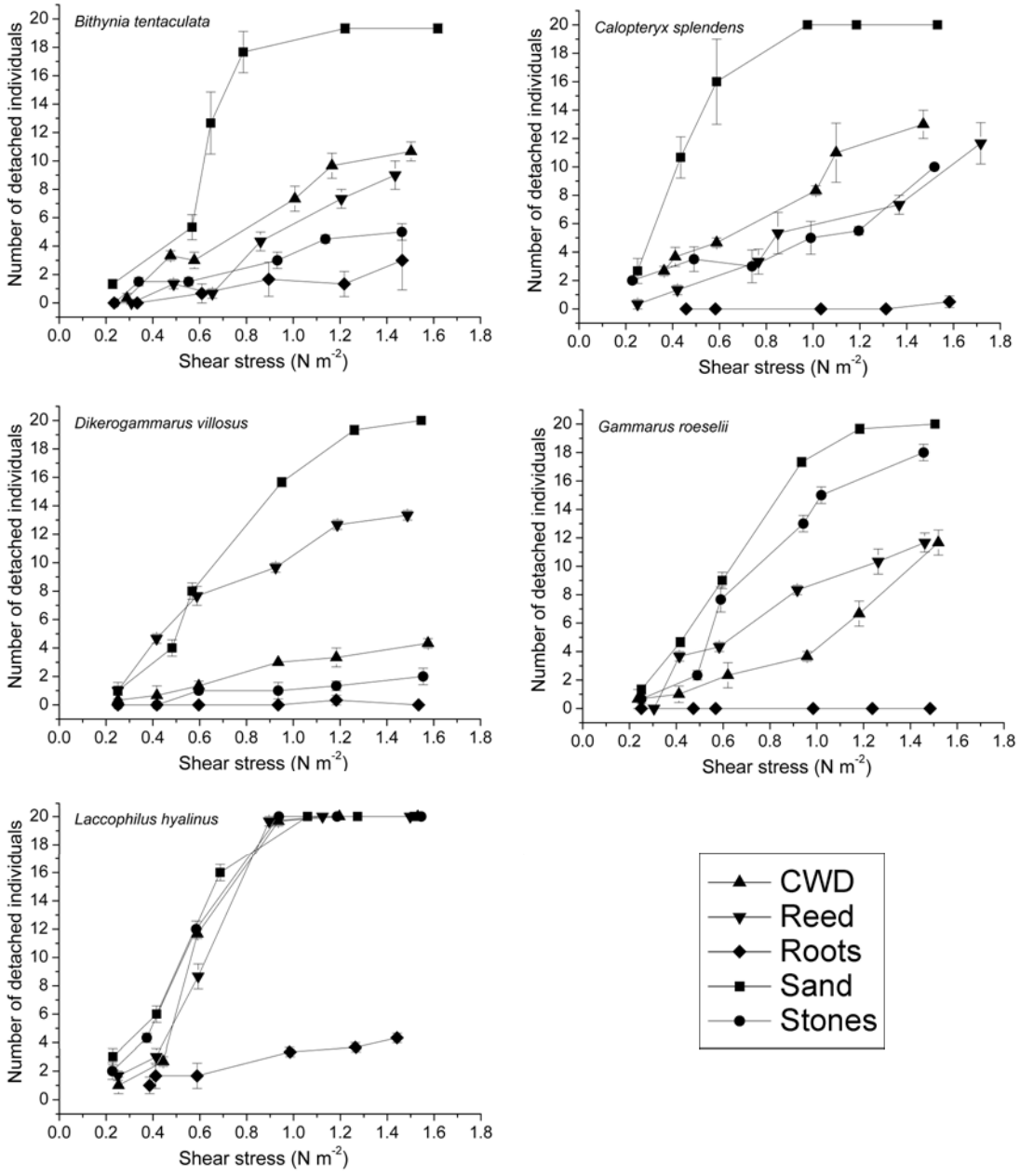

Figure 8: Number of detached individuals from a possible maximum of 20 individuals in each habitat for the five species studied, as a result of applied shear stress caused by ship-induced waves. Plotted values represent the mean number of detached individuals (± SE) for three replicates. Results for each habitat are connected by lines. CWD: coarse woody debris.

Table 7: Sigmoid regression analysis ($\ln y = b_0+b_1/t$) between number of detached individuals and shear stress. For each test, the R^2 value (adjusted for degrees of freedom), the corresponding significance levels (*** $p<0.001$, ** $p<0.01$, * $p<0.05$, n.s.: not significant) and the curve coefficients (b_0 / b_1) are given (CWD = coarse woody debris).

Species	CWD	Reed	Sand	Stones	Tree roots
Bithynia tentaculata	0.70*** (-1.7 / 3.8)	0.70*** (-2.1 / 3.4)	0.70*** (-1.3 / 3.2)	0.74*** (-1.4 / 2.8)	0.29* (-1.0 / -0.4)
Calopteryx splendens	0.70*** (-0.6 / 2.9)	0.69*** (-1.3 / 2.5)	0.85*** (-0.7 / 3.6)	0.57*** (-0.1 / 2.1)	0.04 n.s. (-0.1 / -4.1)
Dikerogammarus villosus	0.56*** (-1.5 / 2.4)	0.96*** (-0.8 / 3.2)	0.71*** (-1.4 / 4.2)	0.62*** (-1.7 / 1.3)	0.04 n.s. (-0.2 / -4.0)
Gammarus roeselii	0.45** (-1.2 / 2.5)	0.79*** (-2.3 / 4.6)	0.98*** (-0.9 / 3.7)	0.39** (-1.1 / 3.4)	No individuals detached
Laccophilus hyalinus	0.70*** (-1.4 / 4.3)	0.90*** (-0.8 / 3.7)	0.93*** (-0.6 / 3.5)	0.80*** (-0.5 / 3.3)	0.26 n.s. (-1.1 / 1.8)

The comparison of detachment rates among species showed species-specific responses to wave-induced hydraulic disturbance according to habitat (Table 8). On CWD, most individuals of *L. hyalinus* were detached, followed by *C. splendens, B. tentaculata*, *G. roeselii* and *D. villosus*. On reed, *L. hyalinus* detachment was highest. On stones, most individuals of *L. hyalinus* were detached; 10 times more individuals of *G. roeselii* were detached than *D. villosus*; intermediate detachment rates were observed for *B. tentaculata* and *C. splendens*. On sand and tree root habitats, which exhibited the minimum and maximum detachment rates, respectively, detachment rate variability among species was lower than in the other habitats (Table 8).

Table 8: Mean number of detached individuals (average across replicates ± SE, n = 3) for the cross combinations of species and habitats studied (CWD = coarse woody debris).

Species	CWD	Reed	Sand	Stones	Tree roots
Bithynia tentaculata	5.7 ± 1.8	2.1 ± 0.8	12.6 ± 3.3	2.1 ± 0.9	0.8 ± 0.5
Calopteryx splendens	8.1 ± 2.3	2.4 ± 0.8	14.9 ± 3.1	7.1 ± 1.6	0.1± 0.1
Dikerogammarus villosus	2.2 ± 0.7	8.2 ± 2.0	11.3 ± 3.4	0.9 ± 0.4	0.1 ± 0.1
Gammarus roeselii	4.3 ± 1.8	6.4 ± 1.9	12.0 ± 3.4	9.4 ± 3.0	0.0 ± 0.0
Laccophilus hyalinus	12.7 ± 3.7	12.5 ± 3.6	14.5 ± 3.3	13.2 ± 3.5	2.6 ± 0.7

However, habitat type was the most important factor explaining the number of detached individuals since 77.0% of the variance in detachments was explained by habitat (value corrected for the influence of the species factor), whereas only 46.5% of the variance was explained by species (value corrected from the influence of the habitat factor - full model: $r^2=0.82$, $p<0.001$, N=75; Multiple Classification Analysis).

The number of detached individuals decreased with increasing structural complexity of the habitat, parameterised by its fractal dimension (Fig. 9). Detachments averaged for the five species were significantly negatively correlated to the fractal dimension of the habitats (Spearman's Rho = -0.71, p< 0.001, n = 5), as well as for all species separately. These significant negative correlations ranged from Spearman's Rho = -0.69 (p=0.005) for *D. villosus*, to Rho = -0.97 for *B. tentaculata* (p<0.001), with intermediate negative correlations found for *C. splendens* (Rho = -0.94, p<0.001), *L. hyalinus* (Rho = -0.82, p<0.001) and *G. roeselii* (Rho = -0.70, p=0.004).

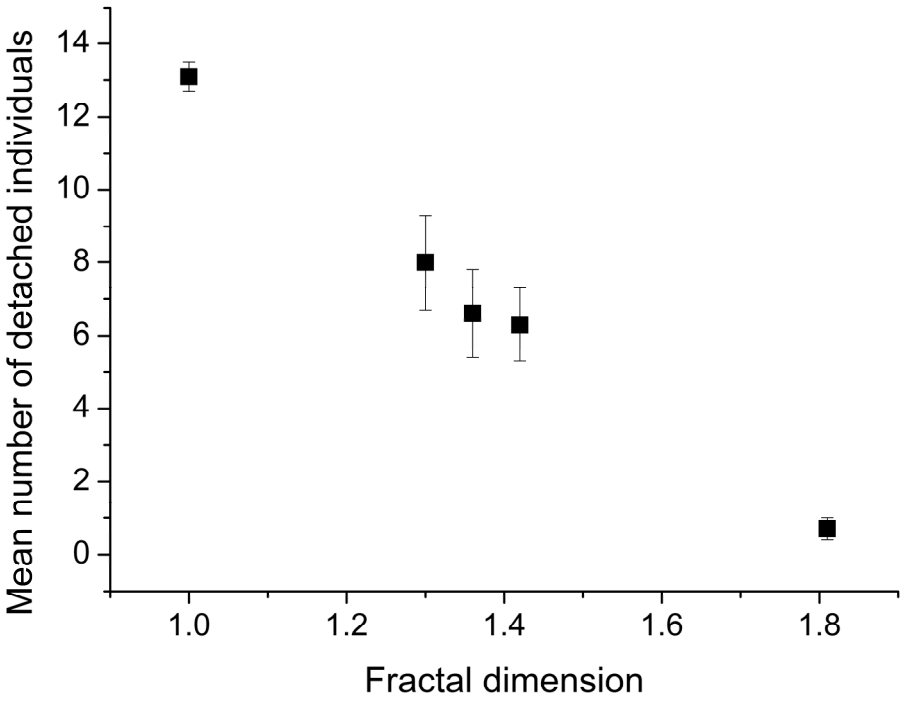

Figure 9: Relationships between mean number (average for the five species ± SE, n = 15) of detached individuals and fractal dimension of the habitats. Fractal dimension represents the 3D-complexity of the habitat, in the following sequence of increasing complexity: sand, coarse woody debris, stones, reed (with a density of 175 stems m^{-2}) and roots.

Effect on navigable surface waters

Shear stresses at which 10%, 25% and 50% of all individuals were detached were exceeded by the passage of the 6.5 m vessel used in our experiments at velocities of 11 km h^{-1} at distances of 35 m and 20 m, and 14 km h^{-1} at 20 m, respectively, from the shore. At a boat speed of 11 km h^{-1}, shear stress decreased by 30% and the detachment of macroinvertebrates decreased by 75% (*L. hyalinus* in reed) when the distance of the passing vessel was increased from 20 to 35 m.

Comparison of invertebrate detachments between field and laboratory flume experiments

Comparing field and flume experiments, three levels of shear stress were applied similarly in both studies: 0.44 versus 0.43 N m^{-2}, 1.21 versus 1.25 N m^{-2} and 1.51 versus 1.48 N m^{-2}, respectively. Hence, invertebrate detachment rates of invertebrates were compared for these three shear stress levels for each habitat. For all shear stress levels and for all habitats, there were no significant differences in the number of detached individuals between laboratory and field experiments, although the number of detached individuals was slightly higher under field conditions (Table 9).

Table 9: Comparison of number of detached individuals in laboratory flume and field experiments (mean ± SD) and results of paired Wilcoxon-tests for sand, coarse woody debris (CWD), stones and reed habitats as well as for tree roots on three shear stress levels. Shear stress levels used for comparisons were low (0.44 N m^{-2} [field] and 0.43 N m^{-2} [laboratory]), medium (1.21 N m^{-2} [field] and 1.25 N m^{-2} [laboratory]), and high (1.51 N m^{-2} [field] and 1.48 N m^{-2} [laboratory]). N=15 for all tests.

Habitat	Shear stress level	Detached ind. in lab	Detached ind. in field	p value	Diff. Z
CWD	***low***	0.33 ± 0.47	2.27 ± 1.36	0.131	-1.511
	medium	5.07 ± 2.92	10.53 ± 6.39	0.138	-1.483
	high	8.53 ± 5.60	12.33 ± 5.77	0.053	-1.923
reed	***low***	0.27 ± 0.43	2.87 ± 1.76	0.102	-1.633
	medium	3.27 ± 3.09	8.13 ± 6.77	0.063	-1.823
	high	5.93 ± 6.44	10.87 ± 6.46	0.052	-1.932
sand	***low***	1.80 ± 0.77	5.13 ± 2.64	0.052	-1.932
	medium	11.4 ± 6.61	18.67 ± 0.33	0.053	-1.923
	high	16.67 ± 3.72	19.87 ± 0.30	0.109	-1.604
stones	***low***	0.67 ± 0.78	2.50 ± 1.87	0.593	-0.535
	medium	5.07 ± 3.05	10.10 ± 7.59	0.053	-1.923
	high	7.13 ± 6.51	11.47 ± 7.87	0.068	-1.826
tree roots	***low***	0.20 ± 0.45	0.33 ± 0.75	0.999	0.000
	medium	0.27 ± 0.43	1.27 ± 1.66	0.109	-1.304
	high	0.40 ± 0.54	1.13 ± 1.83	0.180	-1.342

3.4 Discussion

In developed countries, freshwater ecosystems are subjected to multiple anthropogenic pressures (Dynesius and Nilsson 1994; Giller 2005; Tockner et al. 2010). We were able to demonstrate for the first time, using *in situ* measurements, that ship-induced waves constitute a severe pressure to invertebrates colonizing the littoral zones of inland waterways depending on wave intensities. The extent of these pressures, which were indicated in previous laboratory studies (Gabel et al. 2008b), were verified in the present study using a similar, *in situ* experimental design that allowed manipulation of wave disturbance by holding all other variables constant. Evidence gathered during *in situ* investigations is generally considered more definitive in ecological studies (Hinkelmann and Kempthorne 2008), as the results produced under field conditions are more reflective of real-world conditions (Hairston 1994).

Invertebrate detachment increased as shear stress rose. This effect was mitigated by the structural complexity of the habitat. Habitats with a higher structural complexity provided more shelter from wave exposure for invertebrates since complex habitats reduce the kinetic energy of waves and provide good fixing possibilities for invertebrates (Gabel et al. 2008b).

Navigation rules for navigable surface waters in north eastern Germany allow boat speeds of 12 km h^{-1} inside a 100 m buffer zone along the shorelines in lakes that exceed 250 m in width (WSV unpubl. data). Our study shows that, at 12 km h^{-1}, a boat may generate a wave-induced shear stress of up to 1 N m^{-2}, leading to the detachment of up to 45% of individual invertebrates (averaged over all species and habitats). In a littoral zone regularly exposed to strong ship-induced waves, structurally complex habitats will be reduced or destroyed, as has been shown in reed-dominant systems (Ostendorp 1989). In case only sand and stone habitats will remain, the percentage of detachment at a wave induced shear stress of 1 N m^{-2} would rise to 66.5 % (average over all species on sand and stone habitat). Therefore, a speed limit of 12 km h^{-1} may be insufficient to inhibit strong invertebrate detachments when boats are passing close to the shoreline. Other lakes that are popular for recreational and/or commercial boating have implemented more restrictive speed limits. At Lake Tahoe (California, United States) the speed limit for watercraft is 8 km h^{-1} (5 mph) in a zone extending 180 m from the shore. At Lake Windermere in the British Lake District the speed limit is 9.7 km h^{-1} (6 mph) especially close to the shore or in no wave zones. These speed limits, however, are restricted only to certain areas; higher speed limits are often applicable elsewhere in the same lakes and other lakes. The general speed limit in water bodies of the Lake District is 18.5 km h^{-1} (10 nautical miles per hour) and, on most lakes in the state of Oregon (United States) the speed limit is 16 km h^{-1} [10 mph]. These speeds are high enough to induce substantial adverse invertebrate disturbance.

Outside of the buffer zones and on rivers in north eastern Germany, boat speeds of up to 25 km h^{-1} are often allowed. During the field experiments, the highest shear stress generated by the small vessel reached 1.5 N m^{-2}. However, littoral zones of navigable inland waters are often subjected to higher wave induced shear stress. On the Havel River (north eastern Germany), shear stress caused by ship-induced waves can be as high as 4.2 N m^{-2} (mean shear stress ± SE, 0.83 ± 0.20 N m^{-2}; n=27) for recreational vessels and up to 2.7 N m^{-2} (0.5 ± 0.31 N m^{-2}; n=8) for commercial barges (unpubl. data). Shear stresses exceeding 1.0 N m^{-2} were measured six times a day (from 1200 (noon) to 1800) during September 2008. On the Havel River, the interval between ship passages ranged from only 8.5 min in July to 13 min in September (unpubl. data). As shown by the sigmoid models, at 1.0 and 1.5 N m^{-2}, respectively, on average 45%, and 50 to 100% of the native organisms, are detached, which means that the hydraulic stress resulting from passing vessels probably results in high detachment rates several times a day. Based on these assumptions, more than 15% of *B. tentaculata* individuals, a species typically occurring on stones (Schäfer 1953), would have been detached from stones six times a day during September. For *L. hyalinus*, occurring mainly on macrophytes and stones (Hendrich 2003), more than 98% of the individuals would have been detached six times a day. On the other end of the range, only 5% of *D. villosus* individuals would have been dislodged from stones, and none from tree roots. This is a species that typically is found on stones (Hesselschwerdt et al. 2008) and roots (Devin et al. 2003) especially in the littoral zones of waterways.

We assume that the demonstrated relationships between shear stress, habitat complexity and number of detached individuals reported in this study are applicable to most commercial waterways or recreational surface waters; other research appears to support this proposition. For example, (Verney et al. 2007) determined, on the River Seine, shear stresses as high as 2 N m^{-2} for barge passages. Similarly, on the Göta River in Sweden, shear stresses of up to 3.9 N m^{-2} were associated with ship-induced waves (Althage unpubl. data). The detachment of invertebrates from habitat surfaces due to ship-induced waves, therefore, appears to be a widespread phenomenon.

When invertebrates become detached from a habitat they may not be able to relocate the preferred micro-habitat, and may also face a higher risk from predation (Gabel et al. 2011b). Additionally, growth rate may be depressed by repeated exposition to wave disturbance, which has been observed for native gastropods and amphipods (Scheifhacken 2006; Gabel et al. 2011a). Consequently, dislodgement of invertebrates can result in shifts in invertebrate community composition (Bishop 2004; Bishop and Chapman 2004), thus affecting ecosystem function and health.

Because of the described immediate effects and potential for long-term adverse impacts, a primary goal of waterway management should be to mitigate the strong ecological pressure generated by intensive commercial or recreational navigation. Management strategies may focus on reducing wave generation, effective mitigation of the effects to macroinvertebrates, or both. Complex shoreline habitats, such as dense reed belts or submerged tree roots, can effectively mitigate the adverse effects of ship-induced waves. However, the ability of the habitat structures to withstand repeated heavy wave assaults will also diminish over time, leading to degradation and fragmentation of reeds and tree roots (Ostendorp 1989 and references therein), and thus lower structural complexity. This will eventually compromise the habitat's ability to intercept and dissipate wave energy, which will be accompanied by reduced fixing possibilities for invertebrates. Both detrimental effects emerging from long-term wave disturbance will result in increased invertebrate disturbance under that conditions (Fig. 10).

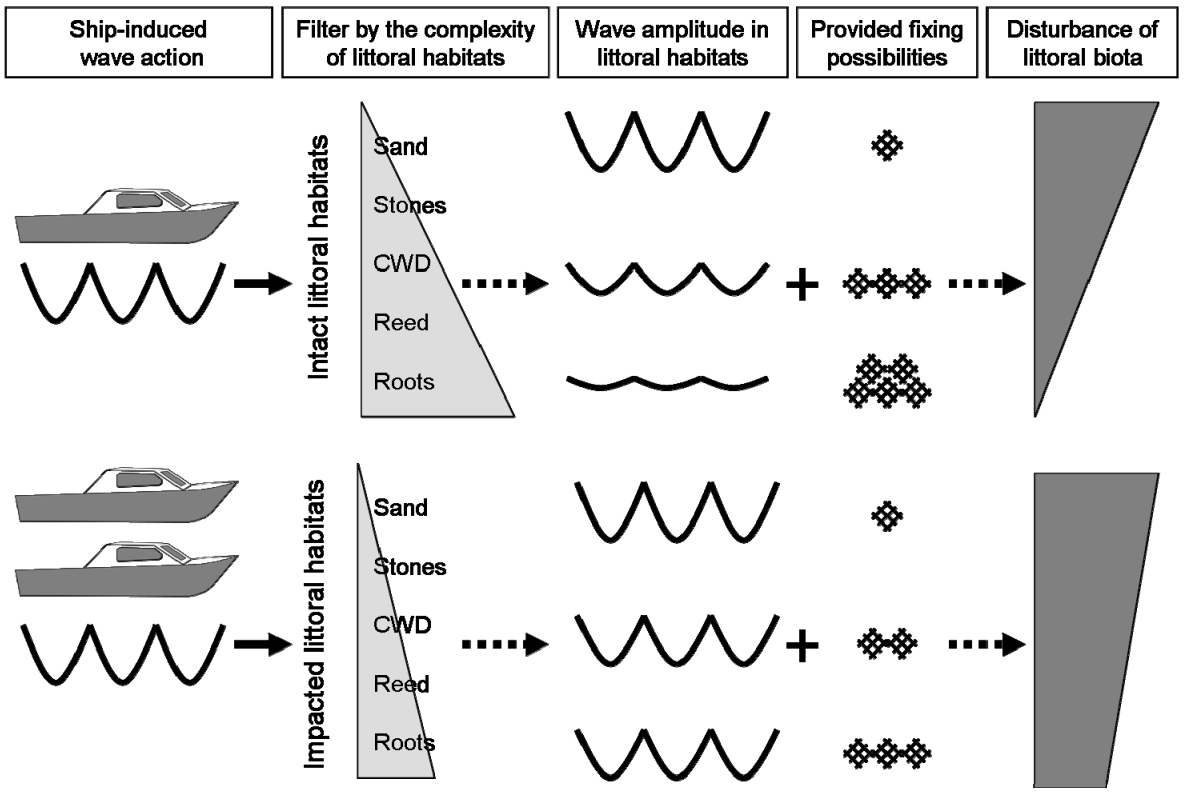

Figure 10: Conceptual representation of the disturbance of littoral biota by inland navigation, its mitigation by habitat complexity (CWD = coarse woody debris; upper part of the sketch), and its amplification by habitat degradation (lower part of the sketch). If littoral habitats are degraded or fragmented due to heavy ship traffic or shoreline development, their structural complexity will be reduced, leading to decreased wave dissipation and less fixing possibilities for invertebrates. This results in an amplification of detachment and disturbance effects on benthic invertebrates.

Shoreline protection such as off-bank revetments or shallow, submerged areas within the water body will reduce wave intensity by breaking the waves and/or increasing dissipation (Wolter et al. 2004; Söhngen et al. 2008; Wolter 2010), thus reducing wave-induced shear

stress. In addition, adjusting navigation rules concerning maximum allowable speed and minimum passing distance may reduce adverse effects on macroinvertebrates. We showed that increasing the vessel to shoreline distance from 20 to 35 m decreased the wave-induced shear stress by more than 30%, and macroinvertebrate detachment by up to 75% (*L. hyalinus* in reed). Moreover, adjusted vessel speeds strongly reduce wave strength (Maynord 2005) and consequently macroinvertebrate disturbance. Improvements in ship design, such as vessel hulls which create less wave action, may contribute to reduced wave disturbance (Sorensen 1973; Day and Doctors 2001; Söhngen et al. 2008).

The results of the field studies described here, may contribute to the development of evidence-based strategies in the management of lotic and lentic shorelines, combining the requirements of navigation and conservation. Along natural water bodies used for inland navigation, no-wash zones should be developed and protected that serve as ecological sanctuaries in order to prevent hydraulic impacts on aquatic biodiversity at ecosystem level.

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4 Waves affect predator-prey interactions between fish and benthic invertebrates

Friederike Gabel, Stefan Stoll, Philipp Fischer, Martin T. Pusch and Xavier-François Garcia

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The first two authors contributed equally to this work.

Abstract

Little is known about the effects of waves on predator-prey interactions in the littoral zone of freshwaters. We conducted a set of mesocosm experiments to study the differential effects of ship- and wind-induced waves on the foraging success of littoral fish on benthic invertebrates. Experiments were conducted in a wave tank with amphipods (*Gammarus roeseli*) as prey, and age-0 bream (*Abramis brama*, B0), age-0 and age-1 dace (*Leuciscus leuciscus*, D0 and D1) as predators. The number of gammarids suspended in the water column was higher in the wave treatments compared to no wave control treatment, especially during pulse waves mimicking ship-induced waves by comparison to continuous waves mimicking wind-induced waves. The resulting higher prey accessibility in the water column was differently exploited by the three types of predatory fish. D0 and D1 showed a significantly higher foraging success in the pulse wave treatment than in the continuous and control treatments. Thereby, foraging success of D0 appears to be achieved more easily since significantly higher swimming activity and foraging attempts under wave treatments were only recorded for D1. In contrast, B0 consumed significantly less gammarids in both wave treatments than in control. Hence, waves influenced predator-prey interactions differently depending on wave type and fish type. It is expected that regular exposure to ship-induced waves can alter littoral invertebrate and fish assemblages by increasing the predation risk for benthic invertebrates that are suspended in the water column and by shifting fish community compositions towards species that benefit from waves.

4.1 Introduction

Predation is a key process shaping terrestrial and aquatic communities and has major consequences on ecosystem functioning (Macan 1980; Sih et al. 1985; Schofield et al. 1988). Predator-prey interactions are influenced by environmental stress such as extreme temperatures, desiccation, habitat modification, and harsh hydrodynamic conditions (Sih et al. 1985). These environmental stresses have complex effects that differ among predator species. For example, increasing flow velocities reduced predation success of invertebrate predators either due to decreased predator-prey encounters (Malmqvist and Sackmann 1996; Hart and Merz 1998; Powers and Kittinger 2002), by altering the ability of predators to chemically detect prey (Powers and Kittinger 2002) or by reducing predators' prey capture success (Peckarsky et al. 1990; Hart and Finelli 1999). Conversely, increased flow velocities can favour predation rates of lotic fish species by increasing food accessibility due to higher drift rates of benthic invertebrates (Elliott 1973); but see (Palmer 1988). However, the benefit for fish is complex and depends on the balance between energy costs and benefits of food intake. For example, growth of Atlantic salmon (*Salmo salar*) increased under high flow velocities due to higher food accessibility (invertebrate drift) but also increased at low flow velocities due to lower swimming costs in comparison to intermediate flow velocities (Blanchet et al. 2008).

Most studies on the effects of hydrodynamic stress were performed in lotic ecosystems. However, hydrodynamic stress also occurs in lakes, in particular in lakes used for commercial or recreational navigation, where wind- as well as ship-induced waves can occur. Wind-induced waves are generated continuously and occur mainly on shores exposed to dominant winds. Ship-induced waves exhibit a pulse pattern generated by the ship passages and can also affect shores that are naturally protected from wind.

The hydrodynamic disturbance caused by wind- or ship-induced waves can dislodge littoral invertebrates from their habitats (Winnell and Jude 1991; Commito et al. 1995; Bishop 2008; Gabel et al. 2008b). Consequently, a higher risk for invertebrates to be preyed can be expected. However, waves may also affect the foraging success of fish predators by influencing swimming performance, displacement, and community shifts (Arlinghaus et al. 2002; Wolter and Arlinghaus 2003; Wolter et al. 2004; Stoll et al. 2010). Stoll and Fischer (2011) distinguished three different reaction types of juvenile cyprinids to pulse waves. While small and fusiform fish (low body depth to fork length ratio) showed increased metabolic rate and somatic growth, small and deep-bodied fish (high body depth to fork length ratio) decreased their metabolic rate and grew less. Larger fish, irrespective of their body shape,

showed increased metabolic rate and reduced somatic growth suggesting that they allocated more energy to swimming activity when exposed to wave action.

In the present study, we experimentally investigated how predator-prey interactions are influenced by hydrodynamic disturbance associated with pulse waves (mimicking ship-induced waves) and continuous waves (mimicking wind-induced waves). Following Stoll and Fischer (2011), we used the same three fish types that differ in their susceptibility to wave disturbance in simulated waves. By quantifying foraging attempts, foraging success and swimming activity of fish predators and suspension rate of their benthic prey, we tested the following hypotheses: i) waves increase prey accessibility, especially under pulse waves as sudden disturbance will detach more individuals, ii) smaller fusiform fish benefit more from hydraulic stress than larger or deep bodied fish iii) ship-induced waves have a stronger impact on predator-prey interactions than wind-induced waves since fish can also forage after a wave passage when prey is still suspended.

4.2 Material and methods

Experimental design

Experiments were conducted in a 10 m long, 1 m wide, and 1 m high wave tank with a glass side wall located at the Limnological Institute of the University of Constance. Near-harmonic waves were created by a pneumatic wave generator placed at one end of the wave tank (Scheifhacken 2006). The waves propagated horizontally for 5.2 m before reaching an artificial shore (slope inclination: 25%) covered with stones and gravel.

A cage was located on a horizontal plane in the middle of the shore. It had a base dimension of 1 m x 0.5 m and was immersed in 0.4 m water depth, providing a total volume of 0.20 m³. The bottom of the cage consisted of sand topped with a thin layer of pebbles (Ø 4-8 mm) as often observed along natural lake shores. To prevent invertebrates and fish from escaping, the walls of the cage were covered with a wire-net of 1 mm mesh size. Water temperature was kept constant (18.7 ± 0.7°C, mean ± SD) during the duration of the study, using a recycling system between the wave tank and a separate heating tank.

Three different wave treatments were run: (i) a continuous wave treatment mimicking continuous wind-waves, (ii) a pulse wave treatment mimicking ship passages, and (iii) a control treatment without waves. The pulse wave treatment consisted of one minute of waves (the wave phase) followed by three minutes without waves (pause phase). Wave hydrodynamic properties were measured inside the cage with an Acoustic Doppler

Velocimeter (ADV, Nortek, Rudd, Norway) at four positions: the front (near side of the wave machine) and rear part (far side of the wave machine) of the cage for each at 6.5 cm and 16.5 cm above the bottom. These depths correspond to the closest location to the bottom within the working range of the ADV and to the furthest location to the bottom which was still under water during wave troughs. To determine current velocity, wave period, and wave length, 100 wave passages were evaluated at each location. Because no significant differences were found in wave characteristics at the four locations (ANOVA, $p > 0.05$ for all tests), we assumed a homogenous wave field inside the cage. Both continuous and pulse waves had an orbital velocity u of 18.5 cm s^{-1}, a wave period T of 1.3 s, and a wave height H of 12 cm, resulting in an energy flux E_F of 21 W m^{-1} inside the cage. Energy flux is assumed to be an appropriate measure of ecological relevance of waves (Hofmann et al. 2008). Thus, wave parameters corresponded with a natural range of energy fluxes (13 to 31 W m^{-1}) as measured for ship-waves at shores of Lake Constance during summer (Hofmann et al. 2008). As wave energy fluxes of the flume were well within the range of natural energy fluxes, and as wave orbital velocities were lower in the flume, effects of flume waves may not overestimate effects presumed in the field. Possible small-scale turbulences generated by the cage or the net were neglected, as observed suspension rates of invertebrates are comparable to those recorded in other flume (Gabel et al. 2008b) and field (Gabel et al unpubl. data) experiments that did not use cages.

Predator and prey species

The amphipod *Gammarus roeseli* Gervais (Crustacea) was used as prey species because it is widespread and common in European lakes and rivers and is a preferred prey for many benthivorous fish species. Furthermore, *G. roeseli* is sensitive to wave-induced disturbance as individuals are detached from their habitat if exposed to waves (Gabel et al. 2008b). *G. roeseli* decreases its activity during day time to avoid predation and hides in crevices and in interstitial spaces between coarser sediment (e.g. Starry et al. 1998) but does not burrow in the sand. Individuals used for the experiments were caught with a hand net on a moderately wave-exposed mixed sand and gravel shore at Lake Constance one week prior to each experiment and stored at 18°C in 20 L flow-through lake water aquariums. To fit with predator feeding requirements, only individuals with a length of 5-7 mm were used for experiments. All predator types fed on and were accustomed to this prey size.

Age-0 and age-1 dace (*Leuciscus leuciscus*, D0 and D1) and age-0 bream (*Abramis brama*, B0) were the predators. Dace and bream are common in central European lakes and rivers. Bream primarily live in lakes and slow-flowing reaches of rivers, and dace live in streams,

rivers, and oligotrophic lakes (Kottelat and Freyhof 2007). Both species feed on gammarids (Hellawell 1974; Hine and Kennedy 1974; Goldspink 1978), picking individual prey items selectively at young age (Bryazgunova 1979; Weatherley 1987) hunting visually during dawn and daytime (Backiel and Zawiska 1968; Crowden and Broom 1980). Thereby, age-0 dace and bream form large shoals with densities up to 20 ind. m^{-2} (dace) or 15 ind. m^{-2} (bream) in Lake Constance (Stoll unpubl. data).

The three types of fish were chosen as each represented a distinct reaction type with respect to somatic growth and metabolic rate when subjected to previous experimental wave treatments (Stoll and Fischer 2011). B0 in the present study corresponds to B0-L in Stoll and Fischer (2011). Individuals of D0 (mean ± SD: 70.44 ± 6.7 mm fork length (FL), 2.5 ± 0.7 g wet weight (WW)) were caught in Lake Constance by beach seining one week before the experiments. D1 (106.1 ± 7.5 mm FL, 8.5 ± 1.8 g WW) individuals were caught by beach seining one year before the experiment and were kept in aquariums for the year. B0 (67.6 ± 9.4 mm FL, 2.3 ± 1.1 g WW) were bred at the Limnological Institute using parents caught from Lake Constance as fish holding history does not influence the susceptibility of these fish categories to waves (Stoll et al. 2008). The three fish types were kept in separate 300 L flow-through lake water aquaria at 18°C and were fed *ad libitum* with living *G. roeseli* daily. To ensure homogeneous hunger levels, fish were starved for 24 hours.

Experimental protocol

Experiments followed a crossed-design between three types of fish (D0, D1, B0) and three wave treatments (control treatment without waves, continuous waves, pulse waves). Each trial lasted for 60 minutes and each treatment was replicated three times. Five individuals of a fish type were used per trial and placed in the cage one day before to start the trial. To acclimate the fish to the start of the wave generator and to experimental waves, fish individuals were subjected to 5 minutes wave pulses every 15 minutes for 3 hours in the morning of the trial. One hour before the trial, a Perspex cylinder corresponding to 10% of the bottom surface of the cage (∅ 25 cm) was placed in the cage and filled with 100 *G. roeseli* individuals. The selected density of gammarids corresponds to densities found in the eulittoral zone of Lake Constance (Mörtl and Rothhaupt 2003). After one hour, the gammarids had settled to the bottom substrate. The cylinder was removed, and a wave treatment was started. At the end of each trial, the fish were removed and immediately killed with 2 mg L^{-1} trichlormethyl-propanol (Carl Roth, Karlsruhe, Germany). Each fish gut was dissected under a stereo microscope (Stemi, Carl Zeiss AG, Jena, Germany), and the number of ingested gammarids

per fish was counted. Gammarids remaining in the wave tank were removed before the next trial.

The number of gammarids suspended in the water column was calculated from high resolution photos taken with a digital SLR camera (Eos 30D, Canon, Krefeld, Germany) placed 1 m in front of the glass side wall of the arena. To gain a high resolution for the images, only one third of the cage volume was photographed. Based on the number of suspended gammarids in the surveyed area, the total number of suspended gammarids was extrapolated for the full cage. Three series of three photos were shot at four intervals during the trials. The time lag between consecutive photos in one series was 0.5 s, the time lag between the different series within one interval was at least one minute. The middle photos of each series were used to count suspended gammarids. The first and last photo in the series was only used to resolve ambiguities on the middle photo to detect movements of gammarids. To test for temporal variability in gammarid suspension throughout the trials photos were taken at four time intervals. During the first four minutes after to the removal of the Perspex cylinder, there was a massive dispersal of gammarids in the cage. These first four minutes were then excluded from the analysis, and the remaining time was evenly divided into three intervals (minutes 5-23, 24-42, and 43-60).

Fish behaviour was recorded by filming trials with a camcorder (NV-GS 280, Panasonic, Hamburg, Germany) placed adjacent to the SLR camera. We assessed fish swimming activity in three equally sized adjacent virtual fields within the cage. The average number of field changes per minute and per fish was counted during three 5-minutes intervals (1-5, 31-35, and 56-60 minutes). Time interval split was different for fish and gammarids because fish were not affected by the removal of the cylinder at the beginning of the experiments.

Foraging attempts were measured by counting the number of snaps for prey made by each fish and expressed as number of snaps per minute and per fish during the swimming activity intervals.

Data analysis and statistics

To evaluate differences in the number of suspended gammarids among time intervals and wave treatments, we used a full-factorial two-way ANOVA. The ANOVA analysis confirmed significant differences in the number of suspended gammarids between the first four minutes and the remaining duration of the trial: all 4 intervals: $R^2 = 0.49$ [wave treatment (df=2, F=5.6, P=0.005), time interval (df=3, F= 37.9, P<0.001), wave treatment x time interval (df=6, F=2.4, P=0.029)] while only intervals from minute 5-60: $R^2 = 0.20$ [wave treatment (df=2, F=6.3,

P=0.003, time interval (df=2, F=2.1, *P*=0.129), wave treatment x time interval (df=4, F=1.0, *P*=0.435)]. Therefore, data of the first four minutes were excluded from further data processing. For the remaining intervals, number of suspended gammarids showed no significant differences among time intervals. Data for these three intervals were pooled for Student's post hoc tests on the effect of wave treatment.

A full-factorial two-way ANOVA was used to assess differences in swimming activity and foraging attempts among wave treatments and among time intervals. Each type of fish was tested separately. For no type of fish did the swimming activity differ significantly among the time intervals (D0: $P = 0.69$; D1: $P = 0.19$; B0: $P = 0.82$), and there was no significant interaction between time interval and wave treatment (D0: $P = 0.89$; D1: $P = 0.93$; B0: $P = 0.83$). Similar results were obtained for foraging attempts among time intervals (D0: $P = 0.09$; D1: $P = 0.97$; B0: $P = 0.93$) and regarding interaction between time interval and wave treatment (D0: $P = 0.15$; D1: $P = 0.55$; B0: $P = 0.61$). Therefore, we removed time interval as a factor from the analyses and left wave treatment as the sole factor. Student's post hoc tests were used for further analysis on differences in swimming activity and foraging attempts among wave treatments.

A full-factorial two-way ANOVA was used to detect effects of wave treatment, fish type and interactions between wave treatments and fish types on foraging success, swimming activity and foraging attempts.

In further analyses, differences in foraging success, swimming activity and foraging attempts among wave treatments were analyzed for each type of fish separately using one-way ANOVAs followed by a Student's post hoc test. Paired samples T-tests were then used to check for differences between the wave phase and the pause phase within the pulse wave treatment. Deviation of the data from normality and homogeneity of variances were tested using Shapiro-Wilk and Levene tests before any statistical analyses which were performed using the software JMP 4.0 (SAS Institute Inc., Cary, NC, USA). Significance was evaluated at $P = 0.05$.

4.3 Results

Impacts of waves on prey

Significantly more gammarids were detached during the pulse wave treatment compared to the control treatment (Fig. 11). No significant differences were detected between the wave (12 ± 6.8 gammarids suspended) and the pause phases (8.3 ± 6.9 in the pause phase, T-Test,

P=0.419) of the pulse wave treatment. The continuous wave treatment resulted in an intermediate number of detached gammarids (Fig. 11).

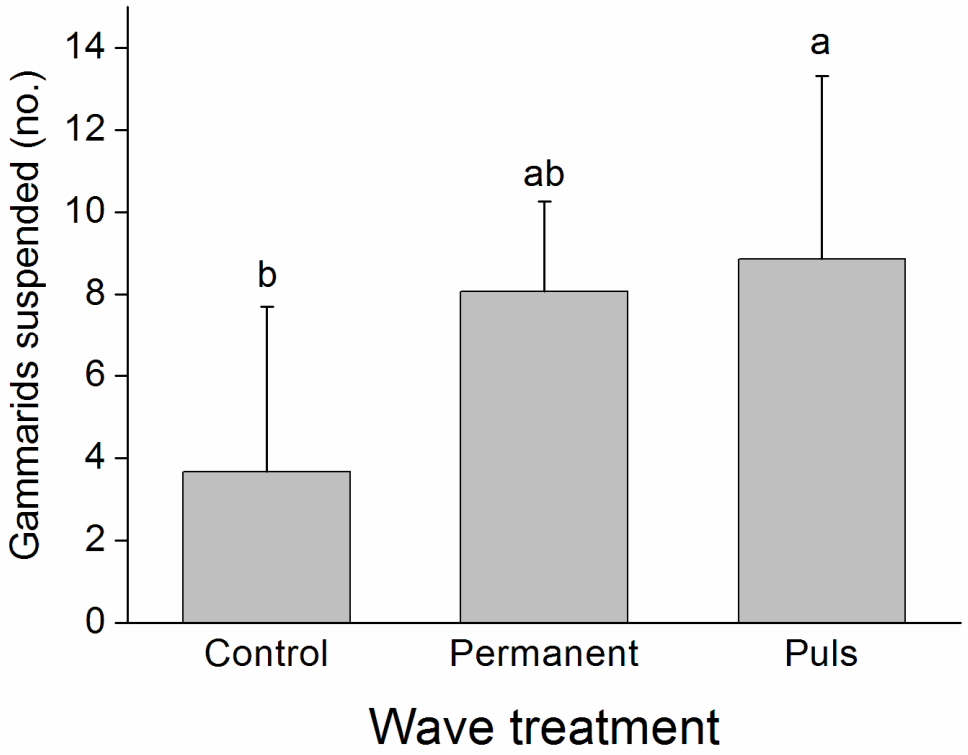

Figure 11: Total number of gammarids (mean + SD) suspended in the water column during the no wave control, continuous wave and pulse wave treatment. Different letters indicate significant differences according to Student´s post hoc tests (*P*<0.05).

Impacts of waves on predators

Significant differences in the number of foraged gammarids among fish types and wave treatments were found (Table 10). Both D0 and D1 consumed significantly more gammarids in the pulse wave treatment than in the continuous wave or the control (Fig. 12a, b). While D0 tended to ingest less gammarids in the continuous wave treatment (2.5 ± 0.5; mean ± SD) than in the control (3.5 ± 0.7), D1 tended to consume more gammarids in the continuous wave treatment (2.9 ± 0.6) than in the control (1.3 ± 0.4) (Fig. 12a, b) but differences were not significant. B0 consumed significantly more gammarids in the control than in continuous and pulse wave treatments (Fig. 12c), and no significant differences in foraging success were found between continuous and pulse wave treatments.

Table 10: Differences in the number of foraged gammarids, swimming activity and foraging attempts among wave treatments and fish types. There were three wave treatments: no wave control, continuous wave and pulse wave. There were three fish types: D0, D1 and B0. Two-way ANOVA. Significant results ($P<0.05$) are given in bold.

	Factor	*df*	*SS*	*F*	*P*
Foraged gammarids ($R^2 = 0.39$)	Wave treatment	2	275.3	15.15	**<0.001**
	Fish type	2	77.5	4.27	**<0.001**
	Wave treatment × Fish type	4	373.9	10.28	**<0.001**
Swimming activity ($R^2 = 0.64$)	Wave treatment	2	200.5	22.8	**<0.001**
	Fish type	2	33.9	3.9	**0.028**
	Wave treatment × Fish type	4	19.0	4.3	**0.005**
Foraging attempts ($R^2 = 0.47$)	Wave treatment	2	4.9	9.4	**<0.001**
	Fish type	2	2.7	5.3	**0.009**
	Wave treatment × Fish type	4	2.7	0.7	**0.046**

Fish swimming activity differed significantly among fish types and treatments (Table 10). Swimming activity of D0 did not significantly differ among wave treatments (Table 11, Fig. 12d), but it significantly differed among wave treatments for D1 and B0 (Table 11, Fig. 12e, f). D1 were least active in the control and most active in the pulse wave treatment. Intermediate activities were recorded in the continuous wave treatment (Fig. 12e). There were no significant differences between the two phases of the pulse wave treatment (Table 11). B0 individuals were significantly more active during the pulse wave treatment than during any other treatment (Fig. 12f). Considering the two phases of the pulse wave treatment separately, B0 was significantly more active in the pause phase than in the wave phase (Table 11). The activity in the pause phase even exceeded the activity in any other treatment. The lowest B0 activity level was recorded in the continuous wave treatment (Fig. 12f).

Table 11: Differences in foraging success, swimming activity, and foraging attempts among the different wave treatments for the three types of fish: age-0 dace (D0), age-1 dace (D1), and age-0 bream (B0). One way ANOVA. Significant results ($P<0.05$) are given in bold.

Foraging success

Type of fish	*df*	*SS*	*F*	*P*
D0	2	70.1	24.1	**0.001**
D1	2	41.7	12.1	**0.008**
B0	2	18.0	11.3	**0.009**

Swimming activity

Type of fish	*df*	*SS*	*F*	*P*
D0	2	3663.0	11.6	0.124
D1	2	27366.8	61.3	**<0.001**
B0	2	16419.5	41.6	**<0.001**

Foraging attempts

Type of fish	*df*	*SS*	*F*	*P*
D0	2	2.2	1.5	0.257
D1	2	4.6	19.2	**<0.001**
B0	2	1.3	4.7	**0.022**

Foraging attempts differed significantly among fish types and wave treatments and also significant interactions between wave treatments and fish types were found (Table 10). Foraging attempts varied significantly among the wave treatments for D1 and B0 but not for D0 (Table 11, Figure 12 g-i). However, D0 made significantly more foraging attempts during the wave phase than during the pause phase of the pulse wave treatment (Table 12). For D1, the number of foraging attempts was significantly higher in the continuous wave treatment than in the pulse wave treatment or in the control (Fig. 12h). B0 had significantly more foraging attempts in the control and continuous wave treatment, than in the pulse wave treatment (Fig. 12i).

Table 12: Differences in swimming activity and foraging attempts between the wave phase and the pause phase of the pulse wave treatment for the three types of fish: age-0 dace (D0), age-1 dace (D1), and age-0 bream (B0). This separation was not feasible for foraging success as gut contents were analyzed at the end of the trials. T-Tests. Significant results ($P<0.05$) are given in bold.

	Fish type	Wave phase	Pause phase	*P*
Swimming activity	D0	5.1 ± 2.0	4.6 ± 0.9	0.706
	D1	7.8 ± 3.3	9.4 ± 4.9	0.732
	B0	3.6 ± 0.9	9.5 ± 1.9	**<0.001**
Foraging attempts	D0	2.6 ± 2.2	0.6 ± 0.7	**0.006**
	D1	0.7 ± 0.3	0.3 ± 0.1	0.219
	B0	0.3 ± 0.2	0.3 ± 0.2	0.536

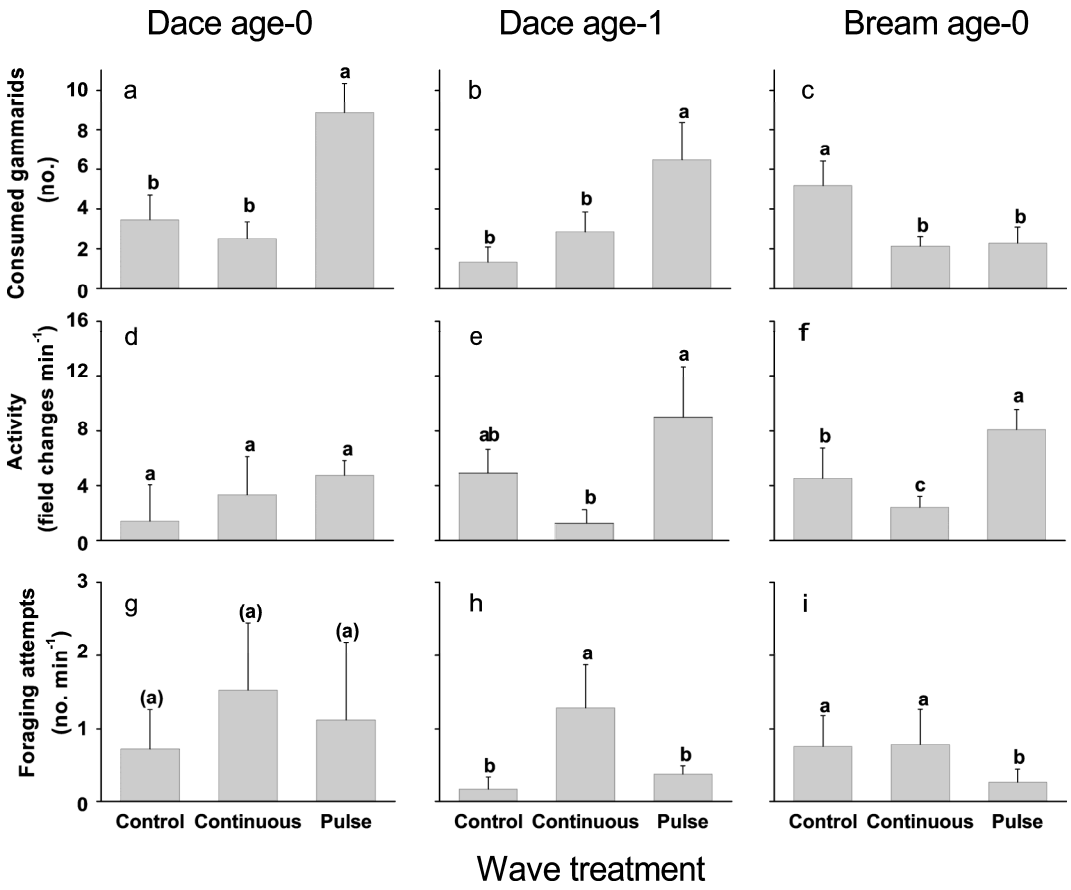

Figure 12: Number of consumed gammarids, fish swimming activity, and number of attempts to capture prey by each individual of dace age-0 (D0), dace age-1 (D1) and bream age-0 (B0) (mean + SD) in no wave control, continuous, and pulse wave treatment. Different letters indicate significant differences according to Student´s post hoc tests (P <0.05).

4.4 Discussion

Impact of waves on prey

In accordance with our first hypothesis, waves increased the number of gammarids suspended in the water column, which left them more exposed to predation. The pulse wave treatment resulted in more suspended gammarids than the continuous wave treatment. Thus, gammarid detachment was not only caused by wave intensity, which was similar among wave treatments, but also by the discontinuity of the disturbance. When exposed to waves, gammarids hid between pebbles to minimize hydrodynamic exposure and to reduce the risk of being suspended. In the continuous wave treatment, the gammarids remained hidden. In the pulse wave treatment, gammarids left their shelters during wave pause phases, letting them exposed and unprepared when the next wave occurred. The observed number of suspended gammarids did not change during the pulse wave treatment suggesting that individuals did not acclimate to the repeated disturbance. Moreover, we observed that individuals remained suspended after the end of the pulse waves.

At orbital wave velocities of 18 cm s^{-1} (corresponding to waves generated by small recreational boats (Gabel, unpubl. data)), about 10% of the gammarids were suspended. Comparable detachment rates were recorded in a smaller experimental wave tank (Gabel et al. 2008b) and under field conditions (unpubl. data) at the same wave velocity. Similarly, Bishop (2008) showed that experimental ship waves dislodged invertebrates from seagrass blades. Hence, our results suggest that even ship-induced waves of low kinetic energy significantly increase predation risk of benthic invertebrates with limited attachment capabilities.

Impact of waves on predators

In agreement with hypothesis two, smaller fusiform fish perform better under waves than larger or deep bodied fish. Dace had significantly higher foraging success in the pulse wave treatment than in the continuous wave treatment, indicating that dace mainly catch prey items during pauses in between wave pulses. Under continuous waves, both dace and detached gammarids were constantly shifted around, reducing the snapping accuracy of the predators which could lead to the high number of foraging attempts under continuous waves as not every attempt might be successful. In contrast, calm conditions during the wave pauses of the pulse waves allowed for more precise snapping. The number of foraging attempts observed was lower during pause phases, probably because after each successful catch, dace required time to accomplish with the prey before they continued foraging (Holling 1959). While D0 foraging success slightly decreased under continuous waves compared to the control, larger D1 had increased foraging success. The difference could result from higher body strength and manoeuvrability of the larger D1, which might lead to more precise snapping even under continuous waves. However, the high foraging success and relatively stable swimming activity of smaller dace under pulse waves indicate that age-0 dace can cope efficiently with wave-induced hydrodynamic disturbance and even profit from the increased food accessibility. It is also known that age-0 dace and other juvenile fusiform fishes prefer wave-exposed shallow littoral habitats (< 50 cm deep, Fischer and Eckmann 1997) and that in these fishes, pulse waves led to increased somatic growth (Stoll et al. 2010; Stoll and Fischer 2011). Larger dace also increased ingestion rates in the pulse waves, but they also increased energy expenditures for activity. Posture stability is directly related to swimming speed in fish (Weihs 1993) which gets increasingly important with body size of the fish, as they gain a larger momentum when seized by waves (Webb 2002). Higher levels of swimming activity and higher energetic costs for posture control are supposed to increase the total energy expenditures for activity in the fish type represented by D1. In the pulse wave treatment, these costs can even outweigh the

benefits from increased foraging success, as these fish grew less in the pulse wave treatment compared to the control (Stoll and Fischer 2011).

B0 did not benefit from either wave treatment. Despite the increased prey availability during wave treatments, B0 had the lowest foraging success. In the wave treatments, foraging attempts and swimming activity were similar or lower compared to the control, except for a significant increase in swimming activity recorded during the pause phase of the pulse wave treatment. Despite an increase in swimming activity, the number of foraging attempts remained low. Thus, this increase in swimming activity was likely a manoeuvre to escape the exposed area before the next wave pulse. Concordantly, B0 exposed to pulse waves had reduced somatic growth (Stoll and Fischer 2011). In lakes, bream leave the shallow littoral zone and move to deeper zones in the middle of their first summer when they become deep-bodied (Fischer and Eckmann 1997).

Finally, also the third hypothesis (ship-induced waves show stronger impacts on the prey-predator interaction than wind waves in a given time interval) was verified. Pulse waves caused more resuspension of gammarids, and feeding success of dace was increased, while it was not in the continuous wave treatment. Also bream changed its swimming activity more drastically in the pulse wave treatment than in the continuous wave treatment in comparison to the control.

These results show how wind- and ship-induced waves affect predator-prey interactions. Waves increase prey accessibility but only favour fish species with body shapes allowing to cope with a harsh hydraulic environment. Moreover, the benefit for individual growth results from a balance between energy intake and energy cost for hunting activity, which appears to be positive only for young fusiform fish represented in our experiments by age-0 dace.

Predator-prey interactions and consequences at higher levels of organisation

Predators and prey responded differently to wave disturbances, and the final effect on the predator-prey interaction depended on how both coped with this stress. When prey is more disturbed than the predator, such as in the gammarid-D0 interaction, the waves are beneficial for the predators. However, when the predator is more affected than the prey, such as in the gammarid-B0 interaction, predation was hampered by waves. In the case of D1, the overall effect of waves on predator-prey interaction was not that clear. Although D1 exerted increased foraging pressure on gammarids in the pulse wave treatment, they grew less because of higher activity costs (Stoll and Fischer 2011). Hence, a predator like D1 seems not to be able to profit from waves on the long term. However, fish are known to take advantage of different habitats

for different ecological purposes (Neverman and Wurtsbaugh 1994; Sims et al. 2006). Hence, by foraging at wave exposed sites, but resting in calm waters, predators like D1 might still benefit from waves.

Besides the direct effects on predator and prey behaviour, waves can also indirectly effect predator-prey interactions by changing predator-predator competition. Under ship-induced disturbance, invertebrates with low fixing or burying capabilities have increased risk of predation. In these circumstances, both invertebrate abundance and species diversity are likely to be reduced. Accordingly, invertebrate species with better hiding capabilities will better cope with wave disturbance and resulting predation. These changes in intra-guild competitiveness and predation pressure will ultimately result in shifts in species composition.

Predator-prey interactions were more strongly affected by ship-induced waves (pulse waves) compared to wind waves (continuous waves). As a consequence, ship-induced waves are expected to cause more pronounced shifts in the community composition of fish and invertebrates inhabiting littoral habitats than wind-waves. In navigational canals, fish species that cannot cope with hydrodynamic stress were shown to be excluded from areas near shipping routes (Arlinghaus et al. 2002; Wolter and Arlinghaus 2003). Changes of littoral invertebrate communities due to wave exposure at wind-exposed shores of lakes (Barton and Carter 1982) and of ship-induced waves (Bishop and Chapman 2004) have been shown. However, under natural conditions, wind induced waves generally occur over longer periods than ship-induced waves, such that in littoral areas that are frequently exposed to wind but rarely to ship waves, wind waves may be ecologically more relevant than ship-induced waves.

Our experimental setup did not control for other environmental conditions induced by waves that may possibly influence predator-prey relationships. In our experiments we used sand and gravel as substrates as they are the common substrates at Lake Constance (Mörtl and Rothhaupt 2003) and other large lakes.

However, structurally complex habitats in the littoral zone may mitigate the wave effects described above. Complex habitats, such as scoured tree roots or dense reed belts reduce the susceptibility to predation (Warfe and Barmuta 2004, 2006; but see Mattila et al. 2008) and dissipate the kinetic energy of the hydrodynamic disturbance (Borchardt 1993; Gabel et al. 2008b). Thus, in structurally diverse littoral habitats, invertebrate densities may not be as strongly affected by the increased predation rate. To avoid shifts in littoral food webs, the management of shores exposed to ship-induced waves should focus on preserving complex habitat structures and reducing shore exposure to waves.

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5 Differential effect of wave stress on the physiology and behaviour of native versus non-native benthic invertebrates

Friederike Gabel, Martin T. Pusch, Philippa Breyer, Vanessa Burmester, Norbert Walz and Xavier-François Garcia

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Abstract

In fresh waters, non-native invertebrate species preferentially spread via navigation waterways, where they often dominate assemblages. Littoral habitats in navigation waterways are regularly exposed to ship-induced waves. We conducted experiments to test the effects of artificial wave exposure on the relative performance of wide-spread native and non-native species. We compared physiological and behavioural response variables (i.e. growth rate, glycogen content, feeding and swimming activity) of two amphipods (native *Gammarus roeselii* and non-native *Dikerogammarus villosus*) and two gastropods (native *Bithynia tentaculata* and non-native *Physella acuta*) subject to wave and control (i.e. no wave) treatment flumes across a six week period. Growth, and in part glycogen content (as a measure of energy storage), were significantly reduced after exposure to waves in native invertebrates, but not in non-native invertebrates. The reduction in growth may be associated with the disturbance effects of waves, such as the higher swimming activity of *G. roeselii* and lower food uptake of *B. tentaculata*. In comparison, the effective hiding behaviour observed for *D. villosus* and good swimming ability of *P. acuta*, were identified as important traits facilitating the successful colonisation of the harsh habitat conditions of littoral waterways. Our study demonstrates that artificial wave regimes may contribute significant selective pressure, thus explaining the observed dominance of non-native species in navigational waterways. The success of non-native species under the harsh hydraulic habitat conditions of these socio-economically driven ecosystems may consequently be traced directly to behavioural and/or physiological traits.

5.1 Introduction

Freshwater environments are particularly affected by biological invasions (Sala et al. 2000; Strayer 2010). For example, there are 432 and 744 records of non-native species that have invaded Europe and North America to date (Strayer 2010). By connecting freshwater systems that were previously separated by natural biogeographical boundaries, artificial navigational waterways form important invasion routes for non-native species, particularly when they include a sea port as entrance gate for non-native species from overseas (e.g. bij de Vaate et al. 2002). Freshwater non-native species may be transported attached to ship hulls (within inland waterway systems) or in ballast water (e.g. Mills et al. 1993; Leuven et al. 2009). Moreover, artificial and natural waterways exhibit altered, and even novel habitat conditions, that are produced by multiple human impacts, which do not necessarily meet the habitat requirements of native fauna. As a result, non-native species are often able to successfully colonise these habitats (Byers 2002), consequently outcompeting native fauna to dominate or even replace existing assemblages in navigational waterways (Borcherding and Sturm 2002).

Several approaches exist to determine which features influence the long-term successful establishment of non-native species in aquatic systems. For example, it is known that successful non-native invertebrates often exhibit ecological traits that may be generally beneficial in disturbed environments, such as short generation time, early sexual maturity, high fecundity and euryhalinity (bij de Vaate et al. 2002). Additional characteristics include high tolerance to changes in temperature and desiccation (e.g. Larson et al. 2009) or to pollution and habitat degradation (Grabowski et al. 2007). However, clarification is still required about why non-native invertebrate species successfully colonise particularly navigational waterways, when arriving in new ranges after transportation by ship or active migration. Waterways are characterised by significantly enhanced levels of hydrodynamic disturbance, due to waves being generated by passing commercial and recreational ships. As a result, ship-induced waves dislodge benthic invertebrates from their habitats (Bishop 2008; Gabel et al. 2008b), thus increasing exposure to predation risk if predators that are able to cope with wave disturbance are present (Gabel et al. 2011b). Furthermore, invertebrates may also require more energy for locomotion in order to return to their initial habitats.

Therefore, we hypothesised that disturbance by ship-induced waves produces a shift in the community composition of benthic invertebrates occupying navigational waterways towards non-native species. Logically, the lower susceptibility of non-native species should be reflected in physiological or behavioural adaptive traits. Hence, we predicted that individual growth rate or energy storage are reduced and swimming activity rates or feeding behaviour

are altered under artificially increased wave regime, for native species but not for non-native species.

5.2 Methods

Experimental design

Experiments were conducted in two artificial flumes (each of 3.0 m length, 0.8 m width, 0.6 m height). Inside each flume, a horizontal plane of 1.6 m length, ending in a 26°slope of 45 cm length, was used as the study area (Fig. 13). Perspex walls longitudinally separated the study area into three compartments, which were used as experimental replicates. Both ends of the study areas were closed with nets (of 1 mm mesh size) to prevent the escape of invertebrates. In each compartment, sand (d_{50} = 2.0 mm) was glued to the bottom and three stones (~13 x 10 x 4 cm³ each) were placed randomly to offer shelter. The indoor flumes were filled with tap water and had a daily light-dark cycle of 14:10 hours. The water level of the study area was 10 cm, while the section in front of the net had a lower bottom, with a water level of 30 cm (following the design of Gabel et al. 2008b). In the wave-treatment flume, a wave generator was installed, while the other flume served as a control without waves. The wave generator created waves automatically by pushing the water mass with a polyvinyl chloride (PVC) plate fixed to an arm, which was operated by a rotating motor (Valeo 15094704, Valeo, Bietigheim-Bissingen, Germany). The duration and strength of movement were regulated electronically by a PDA (FSC Pocket Loox N560, Fujitsu Siemens, Munich, Germany). Waves of 15 s duration were created in the wave flume every 10 min from 06:00 to 20:00 to mimic typical daily navigation traffic in an inland waterway.

To ensure similar experimental conditions in the replicated parts of the wave flume, orbital velocities were determined at seven locations in each compartment using an Acoustic Doppler Velocimeter (ADV; Micro ADV 16 MHz, 50 Hz recording; Sontek, San Diego, CA, U.S.A.). The locations included (1) one directly downstream of the net, (2) one 50 cm downstream of the net, (3) three along a cross section 100 cm behind the net; close to right wall, in the middle and close to the left wall, and (4) one in front of the backward slope. At each point, seven replicated measurements, each of 15 s duration were conducted at 1 cm above the bottom. No significant differences were found among the three compartments at comparable locations (according to ANOVAs with subsequent Scheffé post hoc tests, highest $F = 1.765$, d.f. = 2, $p = 0.193$ at the lowest). Hence, the invertebrates experienced similar mean orbital velocities (31.5 ± 3.9 cm s^{-1}) in all compartment replicates.

Wave orbital velocities, frequency of occurrence, duration and daily timing were similar to wave conditions measured at a North Eastern German river (the Havel River), which is an inland waterway providing access for barges and recreational ships from the North Sea to Berlin. At Havel River, wave orbital velocities of 27.4 ± 15.1 cm s^{-1} were measured, with a frequency of occurrence every 10.3 ± 2.4 min (unpubl. data).

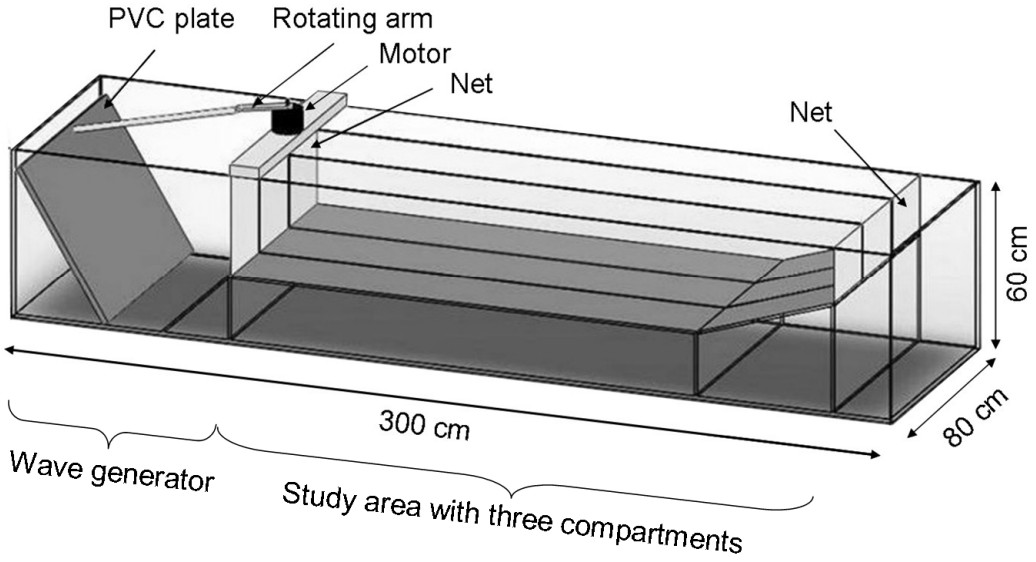

Figure 13: Sketch of the experimental wave flume. A similar set up was used for the control flume except for the wave generator.

Test animals

Experiments were conducted on two groups of native and non-native species that commonly colonise water bodies in central Europe. The first group comprised the native amphipod *Gammarus roeselii* Gervais and the non-native amphipod *Dikerogammarus villosus* (Sowinsky). The second group comprised the native gastropod *Bithynia tentaculata* L. and the non-native gastropod *Physella acuta* (Draparnaud). *Dikerogammarus villosus* originates from the Ponto-Caspian region and disperses mainly through navigational waterways (Holdich and Pöckl 2007). At these sites, *D. villosus* often replaces other amphipods (e.g. Dick and Platvoet 2000; Pöckl 2007). *Physella acuta* specimens observed in central Europe may originate from south east Europe (Cope and Winterbourn 2004) or more likely North America (Dillon et al. 2002; Oscoz et al. 2010). This species spreads via navigation waterways and/or by unintentional release from aquaria (Kinzelbach 1995). *Physella acuta* and *B. tentaculata* co-occur in many lakes and rivers (e.g. Havel River, unpubl. data.). The native and non-native pairs of species selected for the purposes of this study have similar body sizes, and thus should be affected to a similar extent by the hydrodynamic forces created from waves.

Invertebrates were collected by hand nets in the Spree River (*Gammarus roeselii*), at the Lake Mueggelsee outlet (*Dikerogammarus villosus*), in the Havel River, and in the Teltow canal (*Bithynia tentaculata*), and from aquaria populations (*Physella acuta*). The sampling sites of *G. roeselii*, *D. villosus* and *B. tentaculata* are moderately exposed to ship-wave disturbance.

Individuals were sorted by body or shell length, in order to include only individuals of comparable length in the experiment. The length of all collected individuals was measured from digital photographs (Eos 350 D, Canon, Krefeld, Germany) using Adobe professional (Adobe Acrobat professional 8, Adobe Systems Inc., San Jose, CA, USA). Amphipod individuals were measured from the base of the antenna to the telson, and gastropods from the apex to the most distant point on the shell.

Experimental procedure

In total, 100 individuals of *G. roeselii* or *D. villosus* were placed into each replicated compartment of the control and wave flumes, resulting in a density of 61 individuals m^{-2}. Such amphipod densities are typical in natural environments (Mörtl and Rothhaupt 2003). For the gastropods, 80 individuals of each species were used, corresponding to a density of 49 individuals m^{-2}.

Amphipods were fed *ad libitum* with commercially available frozen chironomids, because *G. roeselii* and *D. villosus* show the highest growth rates when fed with this matter (Gergs and Rothhaupt 2008). Gastropods were fed *ad libitum* with dried fish flakes and lettuce (Brendelberger and Jürgens 1993). In addition, the animals were able to graze on biofilm growing on the stones and flume walls, or feed on suspended particles.

Water temperature was maintained at a constant 14°C for the amphipods, and 18°C for the gastropods. Each experiment lasted six weeks. Body length and dry mass of invertebrates were measured biweekly from 10 randomly chosen individuals from each replicated compartment. Body length was measured from digital photographs, following the same method used for the size selection of invertebrates before the start of the experiments. Dry mass was determined by drying individuals separately at 60 °C overnight and weighing them to the nearest 0.01 mg on the following day.

Activities of test animals

The swimming and feeding activity of amphipod individuals were estimated by recording the time (in seconds and minutes, respectively) that each active individual (n > 39 observations per hour) spent swimming in the water column or feeding on provided chironomid prey. Twice a week direct visual observations and time records were collected for a one hour period at each replicate flume. The behaviour of gastropods was assigned to three categories: (1) inactive, with only the shell being visible, (2) active, when gastropods exposed their foot, head and/or tentacles but without locomotion, and (3) crawling, when gastropods moved through the flume on their feet. The status 'active' was interpreted as suspension feeding for *B. tentaculata* (Brendelberger and Jürgens 1993). The frequency of each activity type was determined relative to the total number of visible individuals (each time more than 90% of remaining individuals) at the time of observation once a day.

Mortality rates and physiological status

At the end of the experiments, mortality rates were determined. We counted the number of living individuals, and estimated mortality rates (in %) as the difference between the initial numbers and the remaining individuals at the end of the experiments, minus the individuals previously removed for analyses. Newly hatched individuals were excluded from analyses.

The physiological status of surviving individuals was estimated based on the glycogen content of body tissue as glycogen is an important indicator for environmental stress (Buckup et al. 2008). Due to the minimum content necessary for glycogen analyses, the use of larger individuals than for other observations were required. For gastropods, the larger individuals (starting length c.f. 1.2 cm) were included in the same experiments as the smaller ones. For amphipods, the larger individuals (starting length c.f. 1.5 cm) were exposed for four weeks to the same experimental conditions, but in a separate experiment in order to avoid larger individuals cannibalising smaller ones. The glycogen content of entire animals was analysed by spectrophotometry after treatment with anthrone reagent (Roe and Dailey 1966) and expressed as mg of glycogen per g of wet weight. One sample consisted of five individuals, and was measured in triplicate.

Data analyses and statistics

We used a repeated measurement ANOVA to test for the effects of treatment on the body length and dry mass of organisms over time. The Mann-Whitney-Test was used to compare the activity and feeding behaviour of amphipods, in addition to the glycogen content and mortality rates of all four investigated species, between wave and control treatments. Observed differences in behavioural category (active, inactive, crawling) frequencies for gastropods were tested with a Chi²-test. Afterwards, separate Chi²-tests were calculated to determine the presence of significant differences of each category between treatments. All statistical tests were performed in PSAW (Version 17, SPSS Inc., Chicago, IL, U.S.A.).

5.3 Results

Amphipods

For both *Dikerogammarus villosus* and *Gammarus roeselii,* there was a significant increase in body length and body weight in both treatments (wave and control) across the experimental period (Fig. 14, ANOVA with repeated measurements, *D. villosus*: body length: effect of time: df = 2, 8; F = 17.0, p = 0.001; dry mass: time: df = 2, 8; F = 42.9, p < 0.001; *G. roeselii*: body length: time: df = 2, 8; F = 683.1, p < 0.001; dry mass: time: df = 2, 8; F = 398.4, p < 0.001). While in *Dikerogammarus villosus*, treatment had no significant effect on either variable (body length: treatment: df = 1, 4; F = 0.4, p = 0.564; interaction between treatment and time: df = 2, 8; F = 1.1, p = 0.370; dry mass: treatment: df = 1, 4; F = 2.7, p = 0.127; interaction: df = 2, 8; F = 3.2, p = 0.081), the body length and body weight of *Gammarus roeselii* were significantly affected by treatment, and with a significant interaction between treatment and time for body length (Fig. 14, effect of treatment: df = 1, 4; F = 64.8, p < 0.001; interaction between treatment and time: df = 2, 8; F = 9.4, p = 0.008) and dry mass (treatment: df = 1, 4; F = 198.5, p < 0.001; interaction between treatment and time: df = 2, 8; F = 6.3, p = 0.014).

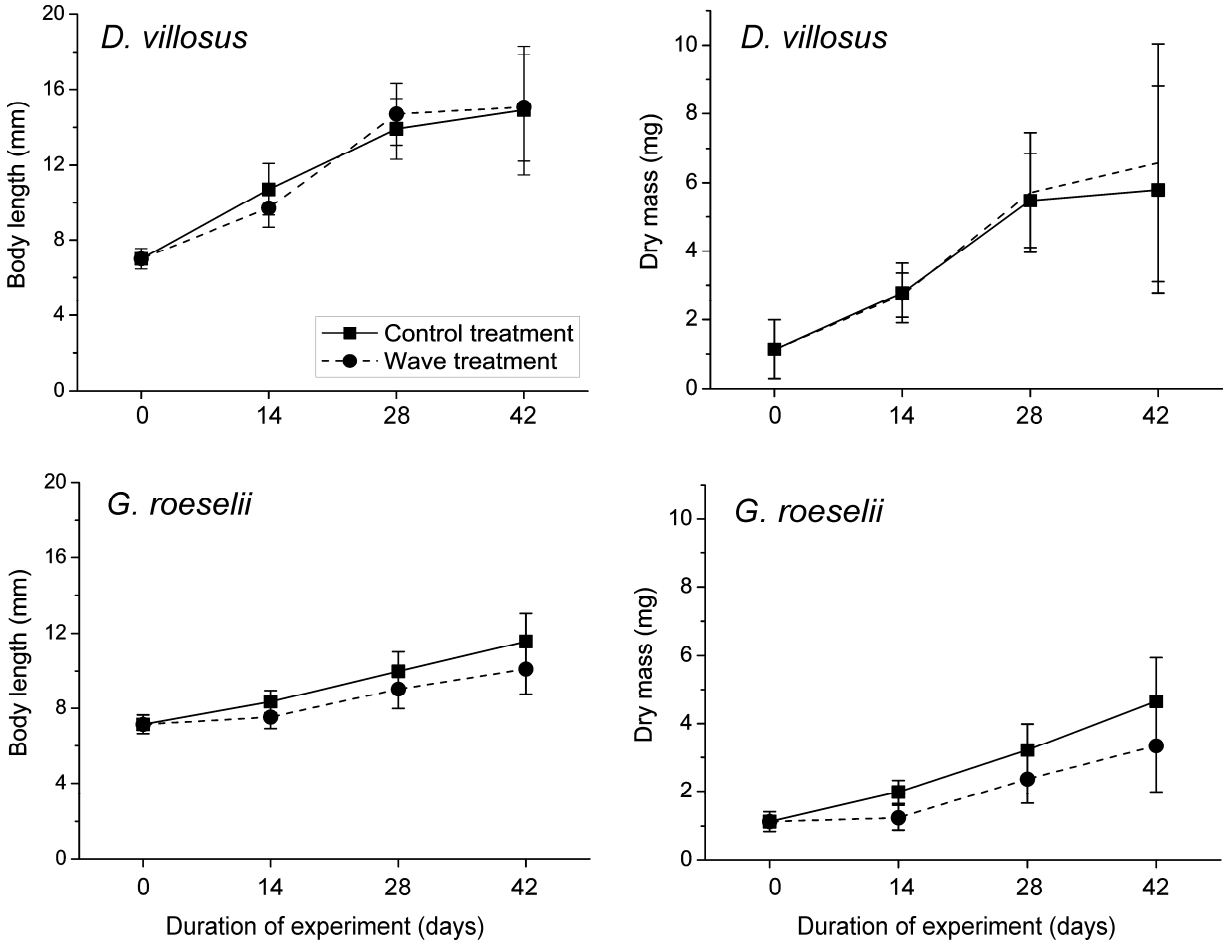

Figure 14: Body length (mm, mean ± SD) and dry mass (mg, mean ± SD) of *Dikerogammarus villosus* and *Gammarus roeselii* in the wave (- -●-) and control (—■—) treatments.

With respect to behavioural and energetic variables, no significant differences between the two treatments were found for *D. villosus* (Table 13). *Gammarus roeselii* also did not show any significant difference between treatments for the time spent feeding. However, this species spent significantly more time swimming in the wave treatment than in the control, and exhibited significantly lower body tissue glycogen content in the wave treatment, which was accompanied by a significantly higher mortality rate of individuals (Table 13).

Table 13: Time spent feeding (minutes, mean ± SD) and swimming (seconds, mean ± SD), mortality rates across six weeks (%, median ± interpercentile range), and glycogen content (mg g^{-1} wet weight, mean ± SD) of *Gammarus roeselii* and *Dikerogammarus villosus* in the wave and control treatments. Note, for technical reasons the glycogen content was determined from larger individuals in a separate experiment. Significant differences between treatments are in bold (df = 1).

Species	Treatment / statistics	Time spent feeding (min)	Time spent swimming (s)	Mortality (%)	Glycogen content (mg g-1)
G. roeselii	Wave treatment	11.1 ± 6.4	18.0 ± 10.2	73.3 ± 11.7	3.3 ± 0.8
	Control	10.4 ± 6.3	11.8 ± 7.4	41.7 ± 11.7	4.8 ± 0.5
	Mann-Whitney U	8575.0	5823.5	0.0	0.0
	p	0.401	**<0.001**	**0.025**	**0.009**
D. villosus	Wave treatment	14.3 ± 9.6	10.6 ± 6.2	47.5 ± 53.3	5.3 ± 0.8
	Control	15.0 ± 9.0	10.7 ± 5.8	34.2 ± 20.0	5.6 ± 0.7
	Mann-Whitney U	2225.5	2296.5	14.5	8.0
	p	0.607	0.834	0.575	0.624

Individuals of *Dikerogammarus villosus* spent most of the time sheltered under the stones that were provided in both treatments. These individuals left the shelter of stones mainly for capturing food. They often capture a chironomid and returned with their prey under a stone to forage. Furthermore, *D. villosus* used the refuges offered by the stones more frequently than *G. roeselii*, and did not increase swimming activity in the wave treatment. In contrast, individuals of *G. roeselii* remained at the place of encounter with prey items and were shifted around with the captured prey when the next wave passed. During waves, and directly after the passage of a wave, many individuals of *G. roeselii* left the bottom and swam through the flume. The duration of these swimming phases was nearly twice as long as in the control (wave treatment: 18.0 ± 10.2 sec, control: 11.8 ± 7.4 sec). Furthermore, only a few individuals sheltered under the stones. Most of the individuals of *G. roeselii* remained on the sandy bottom, or were loosely attached to the stones being occasionally displaced by the waves.

Gastropods

Both in *Physella acuta* and *Bithynia tentaculata* shell length and body weight significantly increased across the duration of the experiment in both treatments (Fig. 15, ANOVA with repeated measurements, *P. acuta*: shell length: effect of time: df = 2, 8; F = 8.7 p = 0.025; dry weight: time: df = 2, 8; F = 6.2, p = 0.035; *B. tentaculata*: shell length: time: df = 2, 8; F = 26.4, p = 0.001; dry mass: time: df = 2, 8; F = 36.5, p < 0.001). While in *Physella acuta*,

there was no significant different in either variable between treatments (shell length: treatment: df = 1, 4; F = 1.7, p = 0.241; interaction: df = 2, 8; F = 0.2, p = 0.651; dry mass: treatment: df = 1, 4; F = 0.1, p = 0.806; interaction: df = 2, 8; F = 0.2, p = 0.853) , shell length and body weight of *Bithynia tentaculata* were significantly lower after six weeks of exposure to wave treatment, with a nearly significant interaction between treatment and time for shell length (Fig. 15, shell length: treatment: df =1, 4; F = 11.3, p = 0.010; interaction: df = 2, 8; F = 2.8, p = 0.136 dry mass: treatment: df = 1, 4; F = 24.9, p = 0.001; interaction: df = 2, 8; F = 4.1, p = 0.059).

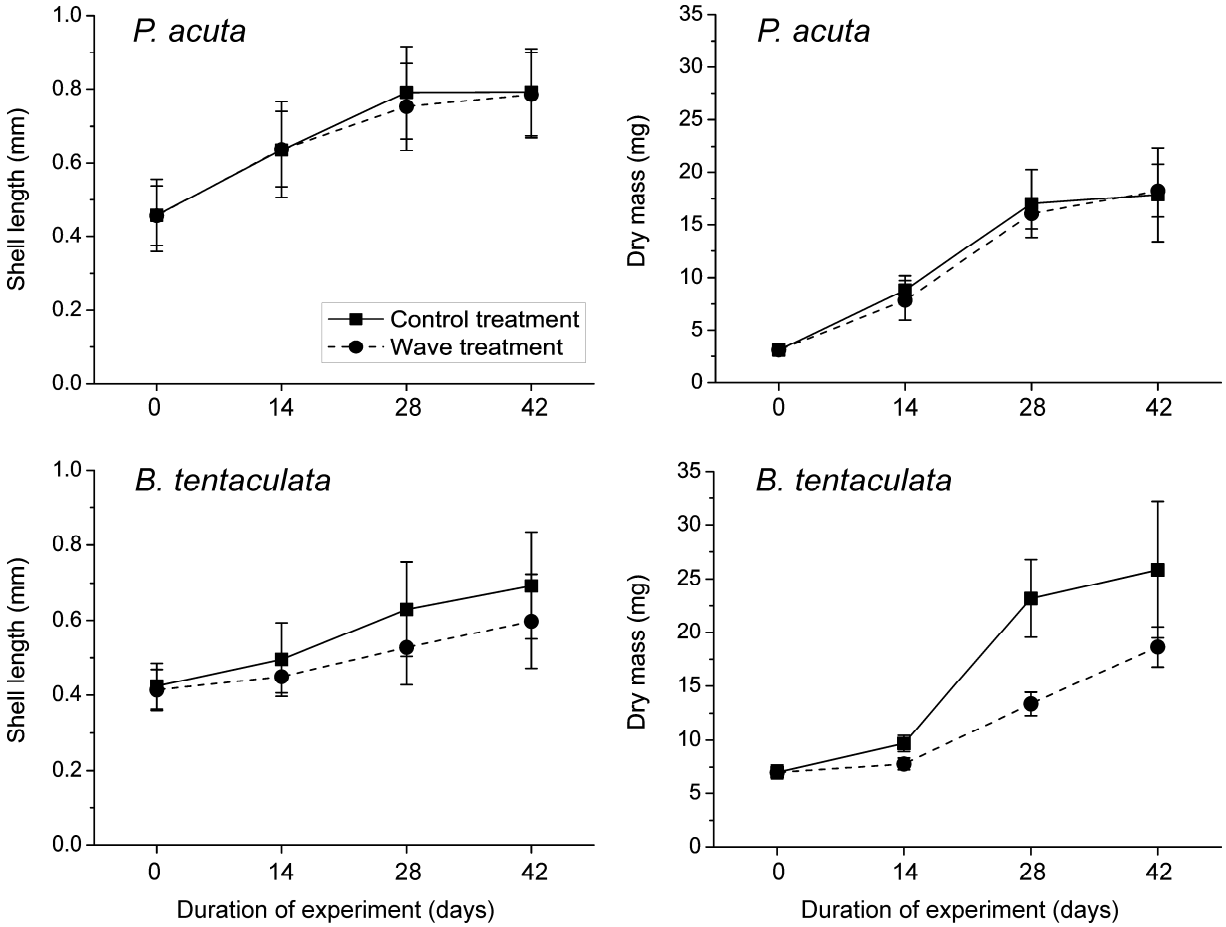

Figure 15: Body length (mm, mean ± SD) and dry mass (mg, mean ± SD) of *Physella acuta* and *Bithynia tentaculata* in the wave (- -●-) and control (—■—) treatments.

For *P. acuta* there was variation in the frequencies of the various behavioural categories (Pearson Chi^2 = 58.6; df = 2; p < 0.001). However, no significant difference was found between the two treatments for any activity (i.e. being active, inactive or crawling), glycogen content or mortality rate (Table 14). The frequencies of behavioural categories (Pearson Chi^2 = 88.8; df = 2; p < 0.001) differed significantly for *B. tentaculata*. Individuals were significantly more inactive and significantly less active when exposed to wave disturbance

(Table 14). Crawling was the only activity type that did not significantly differ between the two treatments. Also, the glycogen content and mortality rate of *B. tentaculata* individuals did not differ significantly between treatments (Table 14).

Table 14: Frequency of activity types (active: tentacles visible; inactive: no tentacles or head visible; crawling) as percentages of total individuals (median ± interpercentile range, chi²-tests), glycogen content (mg g^{-1} wet weight; mean ± SD), and mortality rates across six weeks for *Bithynia tentaculata* and *Physella acuta* in the wave and control treatments. Please note that glycogen content was determined from larger individuals exposed simultaneously to the same experimental conditions. Significant differences between treatments are in bold (df = 1).

Species	Treatment / statistics	Activity (%)			Mortality (%)	Glycogen content (mg g^{-1})
		Inactive	Active	Crawling		
B. tentaculata	Wave treatment	59.6 ± 44.0	30.0 ± 38.9	10.4 ± 14.9	35.0 ± 9.8	16.3 ± 5.8
	Control	24.6 ± 71.4	66.3 ± 65.7	9.1 ± 20.0	33.5 ± 7.0	16.1 ± 5.3
	Test statistics	42.3 [a]	46.3 [a]	0.2 [a]	13.5 [b]	4.0 [b]
	p	**<0.001**	**<0.001**	0.691	0.485	0.827
P. acuta	Wave treatment	26.7 ± 6.0	36.9 ± 17.9	36.4 ± 20.3	40.0 ± 7.0	4.1 ± 2.0
	Control	26.7 ± 49.9	41.1 ± 31.3	32.2 ± 52.7	40.0 ± 5.0	7.1 ± 3.6
	Test statistics	0.006 [a]	0.6 [a]	0.824 [a]	2.5 [b]	2.0 [b]
	p	0.937	0.433	0.364	0.400	0.275

[a] Chi²-Test
[b] Mann-Whitney U-Test

Similar to *D. villosus*, *P. acuta* did not differ in any investigated parameters between wave and control treatments. During the experiments, *P. acuta* often crawled inverted beneath the water surface and moved regularly adhering to the water surface, while *B. tentaculata* adhered to solid surfaces. Furthermore, *P. acuta* reproduced in all compartment replicates of both treatments after four weeks.

5.4 Discussion

There exists broad evidence that anthropogenic pressure to natural ecosystems may favour the invasion and persistent establishment of non-native species by changing habitat conditions (Byers 2002). Habitat conditions in strongly altered socio-ecological systems (Young et al. 2006) are shaped by new combinations of key environmental factors. These conditions are novel both for native species and potential invaders, so that native species often lose their

prior-residence advantage (Byers 2002). Navigation, and accompanying hydrodynamic disturbance due to waves, alters habitat conditions particularly for littoral invertebrate species. Long-term structural habitat degradation combined with the uniformization of habitats due to channelization, shoreline modifications and dredging may further aggravate these effects in a cumulative manner.

Our study provides the first experimental evidence that non-native amphipod and gastropod species are less susceptible to anthropogenic wave disturbance than related native species using similar ecological niches. Wave disturbance was found to have an adverse effect on growth and partial energy storage of native invertebrates, while non-native species were not impacted. In the current study, non-native *D. villosus* spent a large amount of time sheltered under the provided stones in comparison to native *G. roeselii*. As a result, this behaviour led to the reduced exposure of individuals to wave stress. This finding supports that of Platvoet et al. (2009a) who demonstrated the efficient use of crevices by *D. villosus* that perfectly suit its body size. Specimens of *P. acuta* that were detached by waves were less disturbed, since in agreement with their natural behaviour they actively move in the water column. For good swimmers, such as *P. acuta*, detachment was obviously less disturbing than for *B. tentaculata*, which is more dependent on contact with solid structures.

Supporting our results for *B. tentaculata*, Scheifhacken (2006) found lower growth rates for native *Radix ovata* under wave conditions than in a control during a two week experiment. High mortality rates and a high number of inactive individuals of *R. ovata* were observed under wave disturbance in these experiments. However, *Radix ovata* is mostly a lentic species (Moog 2002), which might explain the presence of higher mortality rates under wave action. Additionally, Scheifhacken (2006) recorded species growth rates at several water depths to take into account the depth extension of wave disturbance. Growth reduction was significantly lower in 80 cm, when compared to 40 cm or 20 cm water depth. Hence, it seems that the growth of native gastropods is directly affected by the level of hydraulic disturbance.

Active behaviour by individuals of *B. tentaculata*, which is associated with suspension feeding (Brendelberger and Jürgens 1993), decreased by more than 50% for individuals exposed to waves, while grazing behaviour did not increase significantly. Feeding on suspended food leads to a higher net energy gain for animals compared to grazing (Hunter 1975; Tashiro 1982; Tashiro and Colman 1982; Brendelberger and Jürgens 1993), resulting in it being the preferred feeding type when both food resources are available (Höckelmann and Pusch 2000). As a consequence, *B. tentaculata* cannot compensate for lower suspension feeding rates by increased grazing. This may have caused the lower growth rates observed in

the wave treatments, since the time spent suspension feeding by individuals was reduced. However, energy storage and mortality were not affected by waves, suggesting that *B. tentaculata* re-allocated available energy to maintain body functions under wave action at the expense of growth. Consequently, *B. tentaculata* would not be fully excluded from navigation channels by waves-induced hydraulic stress, but would perform better in channels with low intensity navigation.

Therefore, in the current study we showed that both behavioural and physiological traits, which are often strongly linked, may determine the successful invasion of invertebrate species in novel socio-ecological systems. Such species traits have been experimentally investigated for several non-native amphipods and gastropods, with ecological stresses being assessed by comparing the performance of non-native and native species under different environmental conditions (Table 15). All studies concluded that the recorded differences in species traits between native and non-native species could contribute to invasion success. For example, tolerance to extreme or changing chemical parameters, high fecundity and a broad prey spectrum have been recognised as important physiological or life history traits for successful invasion (Table 15). Also, behavioural properties, such as aggressive behaviour, intraguild predation and pronounced predator avoidance, have been shown to facilitate invasion (Table 15). In the present study, we supplemented this knowledge by providing experimental proof that tolerance against hydrodynamic disturbance, which typically occurs in navigational waterways, is a key trait that could alone explain successful invasions of these systems by neozoans.

The observed differences in behaviour and physiology of native and non-native species may result either from pre-adaptations (e.g. Correa and Gross 2008; Cremer et al. 2008; Schlaepfer et al. 2009), from rapid adaptive changes (e.g. Whitney and Gabler 2008; Alford et al. 2009), or from a combination of both (Henery et al. 2010). However, the assumption of pre-adaptation in non-native species should be considered in parallel with the assumption that certain native species may also exhibit pre-adaptive traits, which facilitate the colonisation of strongly altered socio-ecological systems. Thus, the success of non-native species under novel habitat conditions should also take into account that non-native species might have to compete with native species with similar pre-adaptations (van Kleunen et al. 2010).

Table 15: Experimental evidence for physiological and behavioural species traits in non-native amphipod and freshwater gastropod species favouring successful invasions.

Physiological parameters and life history traits

Species traits	Non-native taxon	Reference
Salinity tolerance/Euryhalinity	*D. villosus, Tarebia granifera*	(Bruijs et al. 2001; Miranda et al. 2010)
Wide temperature tolerance	*D. villosus, Tarebia granifera*	(Bruijs et al. 2001; Miranda et al. 2010)
Tolerance of wide variations in oxygen content	*D.villosus*	(Bruijs et al. 2001);
High fecundity and reproductive potential	*D. villosus*	(Pöckl 2007)
Short maturation time and brood development time	*D. villosus, D. haemobaphes*	(Pöckl 2009)
Broader prey spectrum	*D. villosus, Echinogamm. ischnus*	(Krisp and Maier 2005; Platvoet et al. 2009b; van der Velde et al. 2009);
Tolerance of anthropogenic wave stress	*D. villosus, Physella acuta*	this study

Behavioural parameters

Parameter	Non-native taxon	Reference
Aggressive behaviour more pronounced	*D. villosus, G. pulex*	(Dick et al. 1995; Dick and Platvoet 2000; Dick 2008)
Intraguild predation	*D. villosus, G. tigrinus*	(Dick and Platvoet 2000; Dick 2008; Platvoet et al. 2009a)
Predator avoidance behaviour	*E. ischnus*	(Pennuto and Keppler 2008)
Tolerance of anthropogenic wave stress	*D. villosus, Physella acuta*	this study

Conclusions

Our study demonstrates that repeated exposure to ship-induced waves reduces growth, and to a certain extent energy storage, of native amphipods and gastropods, but not of their non-native counterparts. Since this pattern was observed for two different taxonomic groups of different ecological traits and constitutive capabilities to withstand hydrodynamic disturbance, similar principles might also apply to other non-native species belonging to different zoological orders. We present new evidence that one specific form of anthropogenic river use alone could favour non-native species, and how this effect may be mechanistically explained.

The differing vulnerability of native and non-native invertebrates to hydrodynamic stress is expected to shift community composition in socio-ecological aquatic systems towards domination by non-native species (e.g. in Rhine River, Borcherding and Sturm 2002). As non-native species arrive from different biogeographical regions and continents, navigational waterways form an arena where species encounter new competitors in specific environmental conditions that have not been previously met (Young et al. 2006). Hence, strong competitive selection of certain traits is expected, leading to a rapid human-induced evolution of invertebrate communities.

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6 Ship-induced waves alter the community composition of benthic invertebrates and favour neozoa

Friederike Gabel, Mario Brauns, Martin T. Pusch and Xavier-François Garcia

(*in preparation*)

Abstract

Ship-induced waves affect aquatic ecosystems by altering the hydrodynamic regime in littoral zones. However, the long-term effects of ship waves on the community composition of benthic macroinvertebrates have rarely been quantified. In our study, we investigated the macroinvertebrate assemblages along a gradient of wave exposure. Sampling took place on a monthly basis from April to September 2008 in five different habitats (coarse woody debris [CWD], reed, roots, sand and stones) at the Havel River. Principal Coordinate Analysis (PCO) revealed distinct community compositions at highly exposed sites compared to intermediately exposed and not exposed reference sites. There was a decrease in abundances of 7 taxonomic groups from a total of 15, especially insect taxa, while abundances of Crustacea increased with increasing exposure to ship-induced waves. Furthermore, abundances of non-native individuals were significantly higher at exposed sites than at reference sites. Habitat specific analyses showed that wave effects were lowest on sand, possibly due to a dominance of ubiquist species, while community structure on other habitats reflected wave disturbance. Tree roots, however, showed lowest effects of waves in respect to functional feeding groups (FFG).

This study documents that ship-induced wave disturbance is detrimental for most taxa of benthic macroinvertebrates colonising littoral zones of navigational waterways. Conclusively, management should consider ship-induced wave disturbance as a severe anthropogenic stressor, especially regarding invasion by neozoa.

6.1 Introduction

Inland surface waters are used for navigation for millennia e.g. documented by the construction of the navigable Shatt-el-hai canal, linking the Tigris and Euphrat rivers in Mesopotamia around 2200 B.C. (Galil et al. 2007). Inland navigation is associated with strong anthropogenic alterations of surface waters such as channelization, dredging, shoreline development, construction of marinas, destruction of natural habitats by mooring and anchors (Lloret et al. 2008) with subsequent effects on water quality (e.g. Adams et al. 1992; Mosisch and Arthington 1998; Nehring 2000). The connection of previously separated water bodies for commercial navigation by channels increased the dispersal of non-native species (bij de Vaate et al. 2002; Nehring 2005; Leuven et al. 2009) and facilitated the exchange and possibly the homogenisation of fauna (e.g. Kinzelbach 1995; Pysek et al. 2010; Strayer 2010). Furthermore, numerous studies stress that vessels are one of the most important transport and dispersal vectors for non-native species via ballast water transport or hull attachments (Mills et al. 1993; Duggan et al. 2005; Nehring 2005; Hulme et al. 2008; Leuven et al. 2009).

Moreover, ship traffic itself affects aquatic ecosystems by altering the hydrodynamic regime in the littoral zones due to the generation of ship-induced waves. These waves can erode shorelines (Nanson et al. 1994; Environmental agency 1999), resuspend sediments (Garrad and Hey 1987; deWit and Kranenburg 1997; Cyr 1998; Anthony and Downing 2003), uproot and alter the community composition of macrophytes (Liddle and Scorgie 1980; Vermaat and Debruyne 1993; Coops et al. 1996; Ali et al. 1999; Doyle 2001). While several studies illustrated the impacts of ship-induced waves on the distribution (Wolter et al. 2004), fitness conditions (Arlinghaus et al. 2002; Wolter and Arlinghaus 2003), growth (Stoll and Fischer 2011) and survival (e.g. Morgan et al. 1976; Holland 1986) of young fishes, larvae and eggs, the impact of ship-induced waves on benthic macroinvertebrates have only rarely been studied.

Bishop (2004) provided first evidence for alterations in benthic assemblages due to ship-induced waves generated by ferries. Comparing the benthic infaunal community compositions of wash and no-wash zones in a tidal river (Paramatta River, Australia), she found lower abundances of some polychaets in the wash zones while other faunistic groups were less affected. However, the applicability of these results to epifauna and freshwaters with ship traffic of various vessel types such as commercial barges and recreational boats is unclear. While infauna mostly does not directly experience wave induced disturbance and might be protected in the sediments, for epifauna greater effects of ship waves are expected as epifaunal individuals are more directly exposed to hydrodynamic disturbance.

In this study, we investigated the effects of ship-induced waves on the benthic macroinvertebrate community composition along a gradient of wave exposure at a large lowland river. We hypothesised that i) differences in benthic macroinvertebrate assemblages will be greatest between highly exposed and reference sites while intermediately exposed communities will be less affected than highly exposed communities and ii) the differences in community structure will be more pronounced for habitats with low structural complexity such as sand, as wave energy is less dissipated and these habitats provide less shelter and fixing possibilities for benthic macroinvertebrates. Furthermore, we hypothesised that iii) neozoa will be more abundant at exposed sites than at reference sites since macroinvertebrate community composition could be disturbed or because neozoa might be less vulnerable to ship waves as they often spread via navigational waterways.

6.2 Methods

Study site

The Havel River is a 325 km long lowland river located in North Eastern Germany, which belongs to the Elbe River system (Naumann 1995). It has a catchment area of 24,297 km² (Behrendt et al. 1999), an average slope of 0.13% and an annual mean discharge of 74.2 $m^3 s^{-1}$ with an average flow velocity of 0.1 $m s^{-1}$ (Naumann 1995). The River Havel is intensively used for commercial and recreational navigation and is suitable for vessels with a length of up to 85 m (BMVBS 2008). It is connected with the Black Sea, the North Sea and the Baltic Sea via several canals, respectively, and thus forms a part of the central invasion corridor of Europe (e.g. bij de Vaate et al. 2002). The river is regulated by six locks. The lock closest to the study area counted 8,692 commercial vessels (Wasser- und Schifffahrtsverwaltung des Bundes 2010c) in 2008 when the sampling was conducted. Sampling was conducted between the river kilometre 41 and 43 (52°27' N, 12°45' E). This section is characterised by several islands, bays, back waters (Fig. 16) and a mixture of developed and natural shorelines. Sampling sites cover a gradient of ship-induced wave disturbance produced by varying distance to the navigation line and partially by shelter by islands, which was validated by enduring records of the local wave regime. Three levels of wave exposure were defined and replicated three times each, i) reference sites (labelled as "R", Fig. 16) where wave disturbance was negligible and waves never exceeded a height of 6.0 cm (Fig. 17) ii) intermediately exposed sites (labelled as "I" in Fig. 16) and iii) highly exposed sites (labelled as "H" in Fig. 16). All sites were protected from wind-induced waves as the dominant wind direction is south west and sampling sites were sheltered by shorelines or have a small fetch.

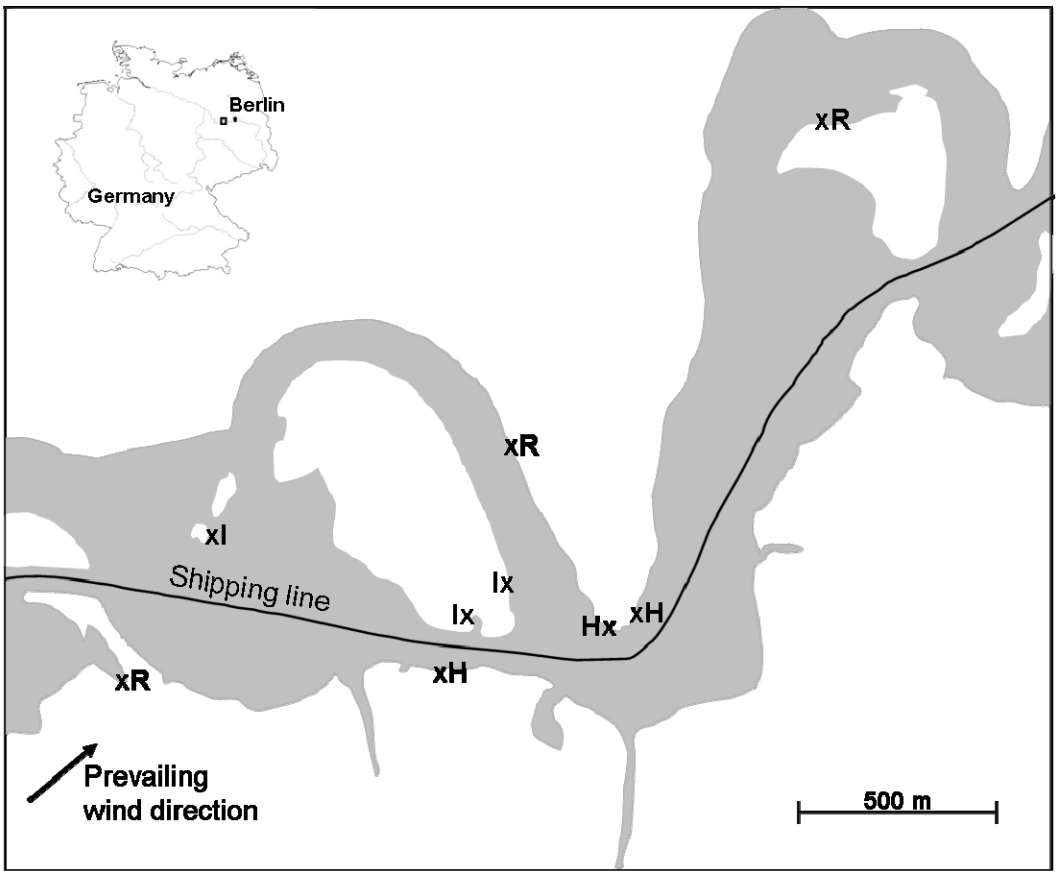

Figure 16: Study site on the Havel River with reference sites (labelled with an "R"), intermediately exposed sites (labelled as "I") and sites highly exposed to ship-induced waves (labelled as "H"). All sampling sites are protected from prevailing winds.

Wave heights were measured from April to October. Three sampling sites were monitored continuously with buried pressure loggers (CAU-T precision pressure transmitters 2nd generation, 10 Hz, Aktiv Sensor, Stahnsdorf, Germany). The remaining sites were monitored successively in a rotating system with two pressure loggers (P-Log520-PA-INT, Driesen + Kern GmbH, Bad Bramstedt, Germany) changing sites after one week. Pressure loggers recorded water level fluctuation greater than the threshold of 4 cm, recording for 5 minutes after triggering. The threshold of 4 cm was set in order to reduce data treatment effort and saving capacity as waves of less than 5 cm height have negligible effects in shallow littoral zones (Hofmann et al. 2008). Additionally, a camera surveyed the navigation channel, taking pictures every 30 seconds to control if waves were generated by ships. Wave heights differed among the level of exposure of the sites (Fig. 17). At reference sites wave heights of 4 to 6 cm were measured on average only 3 times a week. At intermediately exposed sites even waves with a height of more than 16 cm occurred, but quite rarely (frequency 0.44 ± 0.03 per week), while these high waves occurred 10 times more frequently at highly exposed sites (frequency 4.54 ± 0.21 per week). Wave energy ($E=1/8\ \rho g H^2$, where ρ is the density of water [1000 kg m^{-3}], g is acceleration due to gravity [9.81 m s^{-2}] and H is the maximum wave height

in a wave event [m]) calculated for all waves higher than 4 cm for reference sites averaged at 10 ± 8 kg s^{-2} (mean ± SD) per week, for intermediate sites at 732 ± 32 kg s^{-2} per week, and for and highly exposed sites at 1284 ± 161 kg s^{-2} per week (all three exposure levels differed significantly from each other, $p<0.05$ for all tests, Kruskal-Wallis with Dunn's post hoc tests).

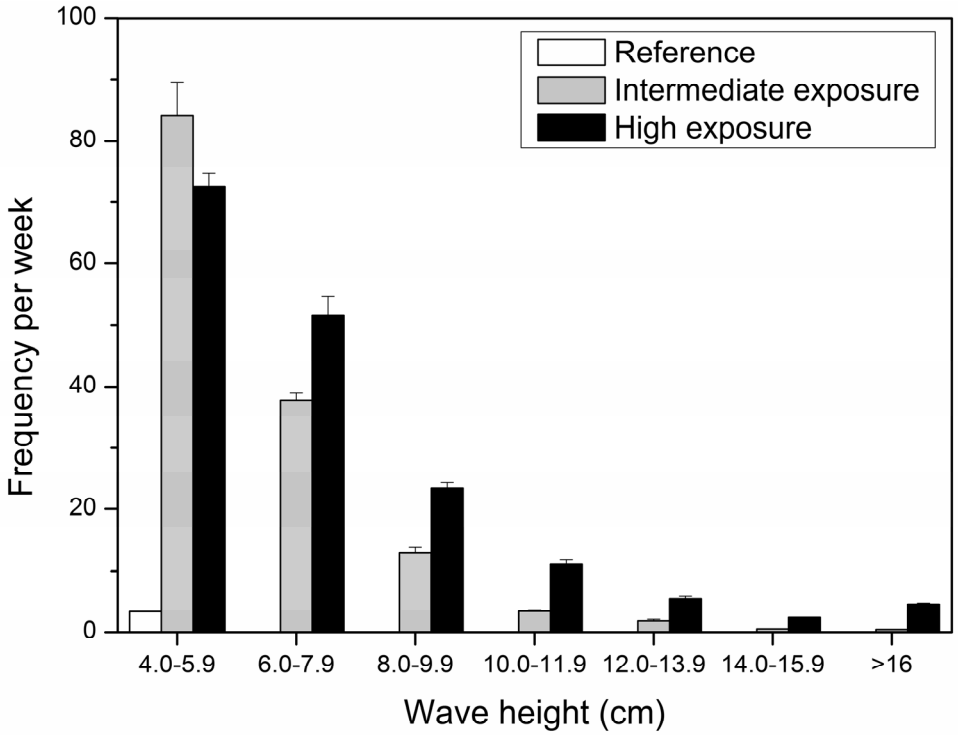

Figure 17: Frequency of occurrence of wave height classes (mean + STD) per week at the reference sites and sites with medium and high wave exposure.

At each sampling site five littoral habitats (coarse woody debris, reed, sand, stones and tree roots) were sampled at a water depth of max. 50 cm. All sampling sites did not differ in abiotic parameters such as water temperature, pH, oxygen content, conductivity and sediment particle size distribution (Table 16) during the course of the study, except for organic matter content in the sediments.

Table 16: Results of Friedman tests for abiotic characteristics at the sampling sites measured from February to October 2008.

Parameter	N	Chi²	df	*p*
Temperature	12	0.409	2	0.815
pH	12	1.167	2	0.558
Oxygen content (mg l^{-1})	12	3.818	2	0.148
Oxygen content (%)	12	1.721	2	0.423
Conductivity	12	2.13	2	0.345
Grain size (d50)	6	2.333	2	0.311
Loss on ignition (%)	6	9.333	2	**0.009**

Sampling of benthic macroinvertebrates

Benthic macroinvertebrates were sampled monthly from April to September 2008 from each habitat separately on a total surface area of 0.2 m^2 each, following the methodology of Brauns et al. (2007). Briefly, we collected samples from CWD and stones by brushing off macroinvertebrates. Reed and roots were sampled with a hand net. Sand was sampled using a Surber sampler modified for lentic conditions (area 0.05 m^2, 500 µm mesh). Habitat-specific samples were preserved in the field in ethanol, and were afterwards processed in the laboratory by sorting, counting and indentifying macroinvertebrates to the lowest feasible taxonomic level: Bivalvia (apart from Sphaeriidae which were identified to genus), Coleoptera, Crustacea, Ephemeroptera, Gastropoda, Heteroptera, Hirudinea, Megaloptera, Odonata, Planipennia and Trichoptera were identified to species level, Diptera to family, Lepidoptera and Oligochaeta were determined to order and Turbellaria were sorted to class.

Statistical analyses

Prior to statistical analyses of macroinvertebrate data, we removed species that were recorded in only one sample from the data set. Species data were expressed as individual densities (ind. m^{-2}) and fourth-root transformed in order to down-weight the effects of highly abundant species (Clarke and Warwick 2001).We used data from individual months as replicates for each site because compositional differences between months were negligible (ANOSIM R = 0.15, P = 0.003).

Differences in the composition of benthic invertebrate communities among the three levels of wave exposure were analysed among sites and among habitats. Compositional differences among sites were tested using analysis of principal coordinates (PCO) in R (R Development Core Team, 2009) and the statistical package Vegan. PCO analysis was followed by an

analysis of similarity (ANOSIM, PRIMER, Version 6, Primer-E Ltd., Plymouth, U.K.). The same set of analyses was conducted for macroinvertebrate communities at habitat scale.

Total densities of invertebrates were compared among exposure levels with an ANOVA (PASW 17, SPSS Inc., Chicago, IL, U.S.A.). Differences in the abundances of the various taxonomic groups among exposure levels were tested via Kruskal-Wallis Tests with Dunn's post hoc tests (GraphPad Prism 4.0, GraphPad Software, San Diego, CA U.S.A,). Indicator species for each level of wave exposure were determined using an indicator species analysis (Dufrene and Legendre 1997; Software package LABDSV in R).

Furthermore, species richness and Shannon diversity were compared among exposure levels via ANOVA with subsequent Scheffè's post hoc tests (PASW 17). Effects of exposure levels on the composition of invertebrate communities of functional feeding groups were evaluated for each habitat according to the database of (Schmedje and Colling 1996). Differences in the proportion of non-native individuals among exposure levels were tested with the non-parametric Kruskal-Wallis test with subsequent Dunn's post hoc test. For all habitats, the proportions of ubiquist individuals were calculated and compared among exposure levels using Kruskal-Wallis Tests with Dunn's post hoc tests. A species was classified as an ubiquist when its stream zone preference was spread over 4 or more zones following the classification of www.freshwaterecology.info.

6.3 Results

Analysis of principal coordinates (PCO) revealed a highly distinct macroinvertebrate community at highly exposed sites that differed significantly from the intermediately exposed as well as the reference sites (ANOSIM R-statistic = 0.49; $p<0.001$ and R-statistic = 0.81; $p<0.001$, respectively; Fig. 18). Intermediately exposed sites grouped closely together but did not separate from reference sites (R-statistic = 0.30; $p<0.001$). However, Shannon diversity was significantly higher at reference sites (2.6 ± 0.1, mean ± SD) than at intermediately (2.0 ± 0.2) or highly exposed sites (2.1 ± 0.0; ANOVA with Scheffè's post hoc test $p=0.033$ and $p=0.019$). Species richness was significantly higher at reference sites (92 ± 13 species, mean ± SD) than at highly exposed sites (69 ± 4 species; ANOVA with Scheffè's post hoc test $p = 0.049$). Species richness at intermediately exposed sites (78 ± 4 species, mean ± SD) did not significantly differ from highly exposed (69 ± 2 species; ANOVA with Scheffè's post hoc test $p=0.519$) and reference sites (92 ± 8 species; ANOVA with Scheffè's post hoc test $p=0.215$).

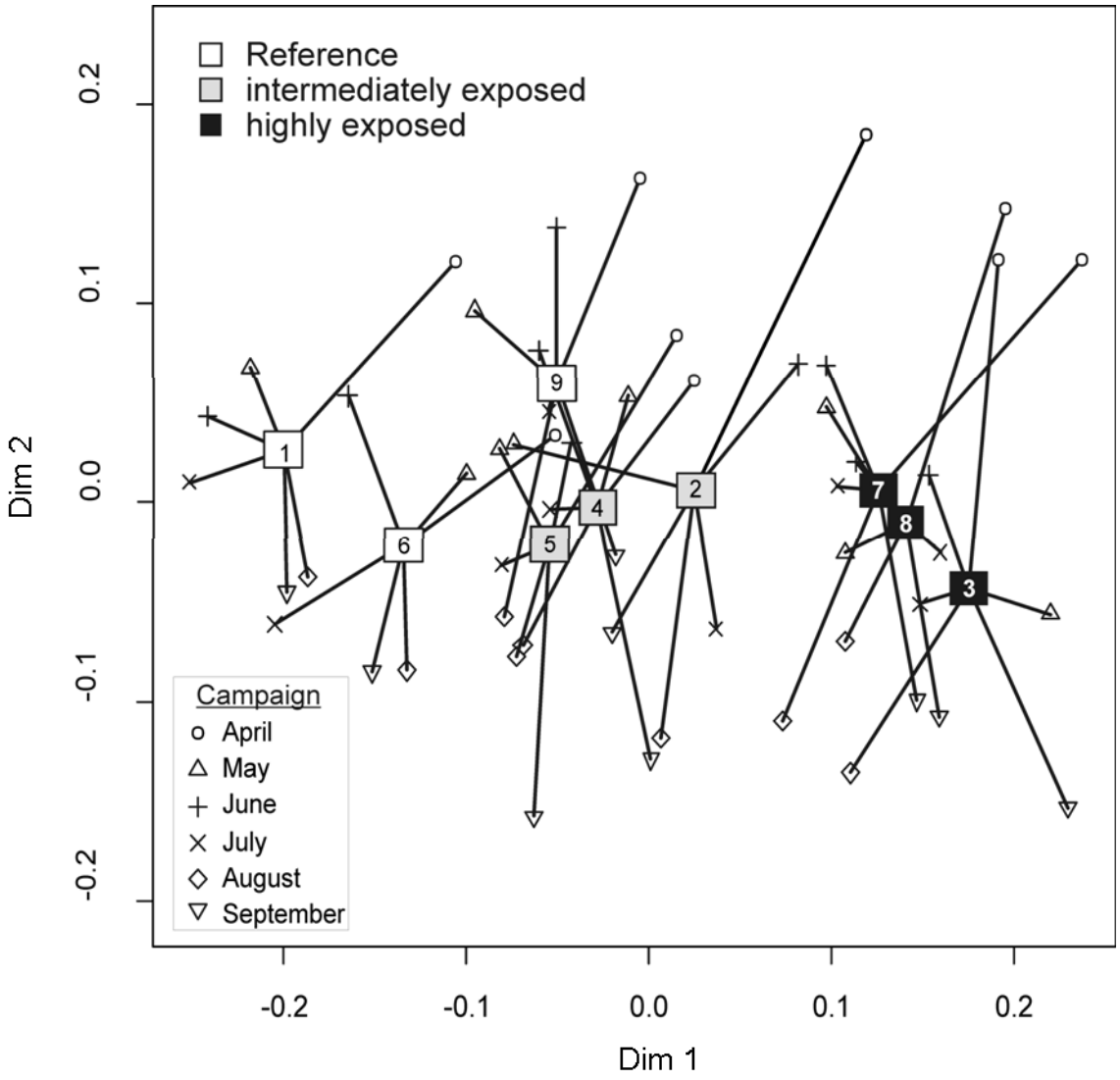

Figure 18: Principal Coordinate Analysis of macroinvertebrate species composition of 4th root-transformed data grouped for all habitats. The closer the squares cluster together, the more similar are the respective macroinvertebrate communities.

Total abundances of macroinvertebrates at highly exposed sites (7,431 ± 547) were comparable with those at reference sites (7,553 ± 1,107) and intermediately exposed sites (p=0.406, ANOVA), which were characterised by slightly higher total abundances (10,182 ± 1,981) due to high abundances of the zebra mussel *Dreissena polymorpha*.

However, 7 out of 15 taxonomic groups had significantly lower abundances at highly exposed sites than at reference sites (Table 17). Especially abundances of Coleoptera, Gastropods (where half of gastropod individuals at highly exposed sites were individuals of the non-native species *Potamopyrgus antipodarum*), Hirudinea, Trichoptera, Ephemeroptera and Odonata were significantly less abundant at highly exposed sites (Table 17). No significant differences along the gradient of wave exposure were found for Bivalvia (dominated by *Dreissena polymorpha*), Crustacea, Diptera, and Oligochaeta (Table 17).

Differences in individual abundances between reference sites and intermediately exposed sites were less pronounced as they were significant only for Ephemeroptera while differences between intermediately and highly exposed sites were significant for Hirudinea, Odonata, Trichoptera and Turbellaria.

Table 17: Abundances (mean ± SE, ind. m^{-2}) of taxonomic groups at highly, intermediately exposed and not exposed reference sites. Different letters indicate significant differences (Kruskal-Wallis Tests with Dunn's post hoc tests).

Taxonomic group	Highly exposed	Intermediately exposed	Reference
Bivalvia	2204 ± 682 a	5003 ± 1851 a	2293 ± 608 a
Coleoptera	1 ±0 a	5 ± 1 a,b	8 ± 2 b
Crustacea	3239 ± 444 a	1842 ± 307 a,b	1382 ± 235 b
Diptera	1285 ± 107 a	1818 ± 322 a	1814 ± 251 a
Ephemeroptera	34 ± 15 a	36 ± 9 a	196 ± 39 b
Gastropoda	319 ± 56 a	535 ± 115 a,b	1105 ± 239 b
Heteroptera	21 ± 6 a	124 ± 114 a	25 ± 7 a
Hirudinea	6 ± 2 a	54 ± 13 b	87 ± 22 b
Lepidoptera	0 ± 0 a	1 ± 0 a	0 ± 0 a
Megaloptera	1 ± 0 a	2 ± 1 a	1 ± 0 a
Odonata	3 ±1 a	22 ± 5 b	58 ± 15 b
Oligochaeta	254 ± 44 a	574 ± 112 a	354 ± 49 a
Planipennia	1 ± 0 a	1 ± 0 a	1 ± 1 a
Trichoptera	52 ± 7 a	139 ± 20 b	212 ± 34b
Turbellaria	12 ± 6 a	29 ± 8 b	28 ± 8 b

Indicator species analysis revealed 25 characteristic taxa for reference sites, e.g. *Ischnura elegans* (Odonata), *Cyrnus trimaculatus* (Trichoptera), *Valvata cristata* (Gastropoda) and *Caenis horaria* (Ephemeroptera) (Table 18), while for intermediately exposed sites only oligochaetes were characteristic. For the highly exposed sites five non-native amphipods were characteristic (Table 18).

Table 18: Indicator species analysis for reference, intermediately and highly exposed sites. Indicator values and level of significance (*** p<0.001, ** p<0.01, * p<0.05) are given.

	Reference	Intermediately exposed	Highly exposed	*Neozoa*
Bivalvia				
Sphaerium sp.	0.57*			
Crustacea				
Asellus aquaticus	0.63**			
Corophium curvispinum			0.66**	yes
Dikerogammarus villosus			0.88***	yes
Echinogammarus ischnus			0.73***	yes
Echinogammarus trichiatus			0.81***	yes
Gammarus tigrinus			0.52**	yes
Obesogammarus crassus	0.54*			yes
Pontogammarus robustoides	0.81***			yes
Diptera				
Ceratopogonidae	0.59*			
Ephemeroptera				
Caenis horaria	0.83***			
Cloeon dipterum	0.71**			
Gastropoda				
Acroloxus lacustris	0.76***			
Bithynia leachii	0.78**			
Bithynia tentaculata	0.65***			
Gyraulus albus	0.55**			
Gyraulus crista	0.61**			
Hippeutis complanatus	0.88***			
Physa fontinalis	0.57**			
Radix auricularia	0.57***			
Stagnicola palustris	0.72***			
Valvata cristata	0.93***			
Hirudinea				
Erpobdella octoculata	0.53*			
Helobdella stagnalis	0.51*			
Hemiclepsis marginata	0.52*			
Odonata				
Ischnura elegans	0.83***			
Platycnemis pennipes	0.62*			
Oligochaeta Gen. Sp.		0.52**		
Trichoptera				
Cyrnus trimaculatus	0.89***			
Mystacides longicornis/nigra	0.60**			
Orthotrichia sp.	0.74**			
Tinodes waeneri	0.51*			

The proportions of individuals of non-native species was significantly higher at intermediately and highly exposed sites than at reference sites (Fig. 19). Especially, the crustaceans *Chelicorophium curvispinum*, *Dikerogammarus villosus*, *Echinogammarus ischnus*, *E. trichiatus* and the gastropod *Potamopyrgus antipodarum* occurred in lower abundances at reference sites.

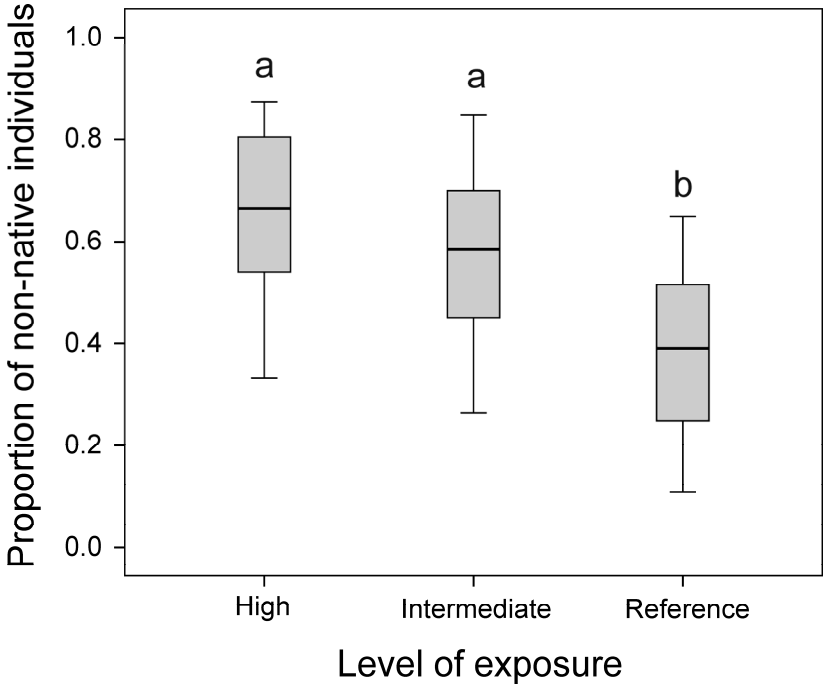

Figure 19: Proportions of non-native individuals at the three levels of exposure to ship-induced waves. Different letters indicate significant differences (Kruskal-Wallis Test with Dunn's post hoc tests).

Habitat-specific analyses

Habitat specific analysis of macroinvertebrate community composition along the gradient of wave exposure showed that macroinvertebrate assemblages of highly exposed sites were distinct from those at intermediately exposed and reference sites for coarse woody debris, reed, roots and stones (Table 19). No effects of waves were found for sand habitats (Table 19). For all habitats except for sand, significantly lower species richness were recorded at highly exposed sites compared to reference sites ($p \leq 0.049$ for all comparisons, vs. $p \geq 0.616$ in sand; ANOVA with Scheffé post hoc tests). On sand, species richness was comparatively low even at reference sites (51 ± 6 taxa on sand versus e.g. 65 ± 12 taxa on reed). The proportion of ubiquist individuals was significantly higher on sand than in the other habitats ($p<0.05$ for all tests, Kruskal-Wallis test with Dunn's post hoc test) where the proportion of ubiquists did not significantly differ among exposure levels ($p>0.05$ for all tests). In contrast to the other habitats, proportion of ubiquists did not differ among levels of exposure on sand ($p>0.05$).

Table 19: Results of habitat specific analysis of differences in macroinvertebrate community composition among exposure levels (ANOSIM).

Habitat	Reference vs. intermediately exposed		Reference vs. highly exposed		Intermediately vs. highly exposed	
	R-statistic	**P**	**R-statistic**	**P**	**R-statistic**	**P**
CWD	0.161	<0.001	0.690	<0.001	0.371	<0.001
Reed	0.28	<0.001	0.655	<0.001	0.393	<0.001
Roots	0.16	<0.001	0.433	<0.001	0.304	<0.001
Sand	0.034	n.s.	0.282	<0.001	0.282	<0.001
Stone	0.189	<0.001	0.601	<0.001	0.554	<0.001

The composition of functional feeding groups significantly differed between highly exposed sites and intermediately exposed sites for three functional feeding groups (Table 20), and 12 FFGs differed between highly exposed and reference sites. In contrast, no significant differences were found between intermediately exposed and reference sites for all habitats. On CWD and stones more functional feeding groups were affected by waves compared to sand, reed and root habitats (Table 20). On CWD the contributions of five functional feeding groups were significantly reduced on highly exposed sites compared to reference sites. On stones abundances of predators, shredders and other FFG were significantly higher while abundances of passive filterer were lower at highly exposed sites than at reference sites. On reed the amount of passive filter-feeders was reduced with increasing wave exposure while scrapers decreased slightly. The great increase of passive filterer on reed resulted from an increase of *Echinogammarus ischnus* (0 ± 0 ind. m^{-2} at reference sites, 19 ± 35 ind. m^{-2} at intermediately exposed and 194 ± 123 ind. m^{-2} at highly exposed sites) with increasing wave exposure. In contrast, on stones there was also an increase of *E. ischnus* with increasing wave exposure but this was counterbalanced by a stronger decrease of the weak passive filterer *Cyrnus trimaculatus* (36 ± 17 ind. m^{-2} at reference sites vs. 0 ± 0 ind. m^{-2} at highly exposed sites). A decrease of the weak third passive filterer of the study sites, *Tinodes waeneri*, also contributed to the decrease of passive filterers at highly exposed stones. In tree roots there were no changes in the composition of FFG along the gradient of wave exposure.

Table 20: Differences for the proportions of functional feeding groups (FFG) in invertebrate communities among the three exposure levels, separated for habitats (ANOVA, Scheffé post hoc tests for fourth root transformed data). Only FFG with significant differences among exposure levels are shown. There were no significant differences between intermediately exposed and reference sites. Cases when FFG at highly exposed sites were significantly lower are indicated by an "l" and when higher by an "h", respectively.

Habitat	FFG	Highly exposed vs. Reference	Highly exposed vs. intermediately exposed
CWD	Active Filterer	0.014; l	n.s.
	Collectors	0.014; l	n.s.
	Parasites	0.014; l	n.s.
	Piercer	0.014; l	n.s.
	Scraper	0.014; l	n.s.
Reed	Passive Filterer	<0.001; h	<0.001; h
	Scraper	0.049; l	n.s.
Roots	[All FFG]	n.s.	n.s.
Sand	Other	0.031; h	n.s.
	Shredder	0.046; h	n.s.
Stones	Other	0.009; h	n.s.
	Passive Filterer	0.044; l	n.s.
	Predator	0.006; h	0.012; h
	Shredder	n.s.	0.014; h

6.4 Discussion

Previous studies have documented that wave disturbance by natural wind waves strongly alter the community composition of benthic macroinvertebrates (e.g. Barton and Carter 1982; Dall et al. 1984; Abdallah and Barton 2003; Scheifhacken et al. 2007).

Our study provides strong evidence that anthropogenic ship-induced waves alter the community compositions of macroinvertebrates and favour neozoa. Most taxonomic groups were severely affected documented by a significant decrease in abundances at highly exposed sites. However, no significant differences between reference sites and intermediately level of disturbance were recorded for Hirudinea, Odonata, Trichoptera and Turbellaria, indicating that many taxa might be able to cope with moderate wave disturbance. Ephemeroptera (especially *Cloeon dipterum*) are nevertheless affected even at low wave disturbance. Ephemeroptera

mainly comprised limnophilic or limno- to rheophilic species, preferring standing or slowly flowing streams (Schmedje and Colling 1996) possibly avoiding sites with high wave disturbance. Taxonomic groups not affected by ship-induced waves comprised many species living in the sediment such as chironomids and oligochaets possibly leading to lower risks of being dislodged and maybe to better escape hydraulic disturbance by diving deeper into the sediment compared to fauna living on the sediment.

Crustacea and Bivalvia were mostly represented by invasive species such as *Dreissena polymorpha* and *Dikerogammarus villosus* which showed to be less affected by wave disturbance. Abundances of Crustacea even increased with increasing wave disturbance. While Bishop (2004) found lower total infaunal abundances at wash zones, there were no differences in total abundances of macroinvertebrates among the different levels of exposure in this study as the abundance of non-native invertebrates increased with increasing wave exposure. However, it still remains unclear if crustacean abundances increased due to decreased abundances in other species letting thus emptied niches or if they are not susceptible to wave disturbance. Experiments with *Dikerogammarus villosus*, however, indicate that this species can cope with wave disturbance as growth and energy storage were not affected when exposed to repeated experimental waves compared to a no wave control (Gabel et al. 2011a). This could also be true for other non-native species. Furthermore, non-native species (*D. villosus*) were shown to use crevices more often and more efficiently than their native counterparts (Platvoet et al. 2009a), which could be beneficial in environments exposed to high hydraulic stress. Furthermore, non-native macroinvertebrates dominate other waterways intensively used for navigation e.g. the main stem of the River Rhine (Borcherding and Sturm 2002).

Contrary to our hypothesis, we did not find more pronounced effects of wave disturbance on habitats with low structural complexity. There were no differences among the levels of exposure on sand, the habitat with the lowest structural complexity. This might be due to the fact that the sand habitat was at all sites dominated by ubiquist species (72-96% of individuals were ubiquists) which colonize a wide range of stream zones with different hydraulic characteristics. The sand habitat was characterised by ubiquistic species, at all levels of exposure and hence there was no effect of wave disturbance as this habitat may be colonized by species able to cope with disturbance at all exposure levels. In accordance with our results effects of wave exposure were not more pronounced on sand than in vegetated habitats on infauna, either (Bishop 2004).

Waves also alter the composition of functional feeding groups (FFGs) of macroinvertebrates on the different habitats. However, there was no increase or decrease of

certain FFGs throughout several habitats. A high diversity of habitats could hence mitigate the alterations in FFGs caused by wave exposure. Especially roots could stabilize the distribution of FFGs with increasing wave exposure as there were no differences in FFGs among the exposure levels in roots. Furthermore, effects of waves were not visible at intermediate wave disturbance. Hence, only greater wave disturbance seem to affect the distribution of FFGs.

The mechanisms leading to alterations of the whole benthic macroinvertebrate community composition due to ship-induced waves are probably complex, depending on interactions between ecological requirements and tolerances of species and habitats. However, for most species direct dislodgement of individuals from their habitats due to hydrodynamic disturbance (Bishop 2008; Gabel et al. 2008b) constitutes a major disturbance due to cascading effects. Dislodgement leads to an increased risk of being preyed by fishes able to cope with wave disturbance (Gabel et al. 2011b). Furthermore, waves were shown to reduce growth rates of macroinvertebrates (Scheifhacken 2006; Gabel et al. 2011a) and to affect energy storage as waves can reduce feeding rates or increase energy expenditure of macroinvertebrates. Furthermore, ship-induced waves might reduce the oviposition of emergent macroinvertebrates as assumed for some trichopterans in the wave swept shores of the Great Lakes (Barton and Hynes 1978).

These disturbances might differ in their extent among species as adaptations to this disturbance can differ among species resulting in shifts of macroinvertebrate community composition. For example, differences in fixing strategy or efficiency and morphological differences, e.g. tenacity strength or foot to shell height ratio might determine species success to cope with wave disturbance (Rilov et al. 2004). Pronounced hiding behaviour can also decrease the adverse effects of waves as was shown for *Dikerogammarus villosus* (Gabel et al. 2011a) leading to changes in the macroinvertebrate community composition.

The alterations of macroinvertebrate community compositions could be even more pronounced in other navigational waterways than in the Havel River since ship traffic in respect to commercial navigation is much higher in other waterways. While on the Havel River (Schleuse Brandenburg) 3 Mio t of goods were transported via commercial navigation in 2009 (Wasser- und Schifffahrtsverwaltung des Bundes 2010c), 152 Mio t and more than 400 Mio t were transported via the Rhine River (Emmerich; (Wasser- und Schifffahrtsverwaltung des Bundes 2010b) and the Mississippi River (US Army Corps of Engineers 2010), respectively. There are more than 12 times more commercial barges passing the Rhine River (Emmerich) and more than 2.5 times more on the narrow Main River (Kostheim, (Wasser- und Schifffahrtsverwaltung des Bundes 2010a) than on the Havel River.

Hence, this intense navigation probably leads to even greater changes and simplifications in the macroinvertebrate community composition than shown in this study. The dominance of non-native species in the main stem of the River Rhine (Borcherding and Sturm 2002) supports this conclusion.

Conclusions

Frequent disturbance by waves severely affects macroinvertebrate community composition, favouring the colonisation of littoral zones by invasive species at sites highly exposed to ship waves. However, lower wave heights seem to affect macroinvertebrate communities less than greater wave heights. Hence, management strategies should aim to reduce ship-induced wave heights and the number of high waves, e.g. by decreased (adjusted) vessel travelling velocities, reduction of number of boats passing by, sailing with great distance to shorelines or supporting the usage of vessels with improved hull design resulting in reduced wave generation. Some of the these management tools concern more recreational navigation, e.g. keeping greater distance to shorelines as they are able to sail also in shallow water, while most of them concern both types of navigation.

Furthermore, preserving the co-occurence of various habitat types and especially the presence of tree roots by appropriate shore protection can mitigate the adverse effects of ship waves on macroinvertebrate communities. However, for several taxa, even low disturbance by ship-induced waves are detrimental. In terms of invasion control, managing ship-induced wave disturbance could play an important role.

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7 General discussion and perspectives

7.1 Rationale and research aims

Inland waters are subjected to multiple anthropogenic stressors (Dynesius and Nilsson 1994; Giller 2005; Tockner et al. 2010). Among them navigation constitutes one of the most severe disturbances, in particular by strong alterations of the local hydrodynamic environment. Commercial and recreational navigation is expected to increase in future, as commercial navigation is considered as the most sustainable mode of transport predominantly in respect to fuel consumption, CO_2-emissions and traffic safety (Rohacs and Simongati 2007; Lambert 2010; Pauli 2010; Radmilovic and Maras 2011). Similarly, recreational navigation is expected to further expand in future as people will have more leisure time (Molitor 2000), and global warming (higher temperatures and less precipitation in summer, IPCC 2007) may increase the number of days when boating is appealing and will attract more people to boating (Loomis and Crespi 1999; Mendelsohn and Markowski 1999; Shaw and Loomis 2008). Hence, hydrodynamic alterations in inland water bodies due to navigation are expected to increase in future as well.

However, the ecological impacts of hydrodynamic alterations, and specifically those of ship-induced waves have rarely been quantified so far. In particular, effects of ship-induced waves on littoral macroinvertebrates, a fundamental link of aquatic food webs providing important ecosystem services (Wallace and Webster 1996; Covich et al. 2004), are poorly understood. Knowledge about the mechanisms of hydrodynamic disturbances is nevertheless essential to assess the effects of anthropogenic alterations on the structure and functioning of macroinvertebrate communities, and to develop scientifically sound management and protection plans.

In this thesis, I used data from mesocosm and field experiments as well as from a field survey to investigate i) the direct and immediate effects of ship-induced waves on benthic invertebrates, ii) the subsequent effects of wave disturbance on the interaction between trophic levels and iii) effects on growth and fitness of benthic invertebrates and iv) the long-term effects on benthic community composition. Furthermore, v) differential effects of ship-waves on native and non-native invertebrates were studied.

7.2 Immediate and short-term effects of wave disturbance on individuals of benthic invertebrates

Ships generate waves leading to hydrodynamic alterations of the littoral environments (Chapter 1). Ship-induced waves can reach considerable wave heights, high velocities and high shear stresses, resulting in shoreline erosion (e.g. McConchie and Toleman 2003) and displacement of fish larvae (Wolter and Arlinghaus 2003; Wolter et al. 2004). However, the effects of wave induced shear stresses on benthic invertebrates have not been quantified yet. In laboratory (Chapter 2) and field experiments (Chapter 3) it was aimed to answer the question what happens to benthic invertebrates when ship-induced waves wash shoreline habitats. In both studies, significant sigmoid-shaped relationships between shear stress and the number of detached individuals were found for most of the habitats. This demonstrates that ship-induced waves constitute a direct and immediate disturbance of benthic invertebrates with a definite pressure-response relationship.

However, the number of detached individuals was much lower in habitats with high structural complexity, as shear stress was more reduced in complex habitats than in simply structured habitats, and since complex habitats provide more fixing and hiding possibilities for invertebrates. Hence, wave disturbance can be mitigated by the structural complexity of the habitat.

In both experiments, I focused on natural habitats which are present at most shores of lakes and rivers in north-eastern Germany. However, if ship traffic is intense or takes place in artificial waterways such as canals, complex habitats are often replaced by artificial shoreline development such as riprap or retaining walls. Assessing the suitability of riprap as a shelter of invertebrates against ship wave disturbance has also been neglected so far, especially because measuring the dissipation of shear stress and collecting invertebrates inside ripraps is challenging. As ripraps consist of habitats with a high structural complexity, it can be assumed that they might provide shelter from hydrodynamic and mechanical disturbance. A first estimation of the suitability of artificial shoreline substrates for sheltering benthic invertebrates against wave disturbance can be assumed on the basis of habitat choice experiments. In these laboratory pre-experiments invertebrates could choose among simply structured sand habitats, a simulated riprap and tree roots in the wave flume (see Gabel et al. 2008a) for being sheltered against wave disturbance. Results showed that invertebrates preferred riprap over sand but tree roots over sand or riprap. Particularly, at high shear stresses invertebrates (especially *Calopteryx splendens*) chose tree roots after having been displaced from riprap. Hence, ripraps could provide better shelter than poorly structured habitats such as sand, stones or coarse woody debris, but could offer less shelter than natural complex habitats such as tree roots.

In contrast, intact retaining walls hardly offer crevices and hiding places for invertebrates, so that disturbance by ship-induced waves is assumed to be very high. Hence, the installation of artificial complex habitats on shorelines dominated by retaining walls could efficiently increase habitat structural complexity, and thus improve the protection of invertebrates against hydrodynamic disturbance. For example, baskets with cement balls were shown to attract invertebrates and were more intensively colonized than simple retaining walls (Schmude et al. 1998). These baskets should also protect invertebrates against wave disturbance more efficiently than bare retaining walls. Moreover, installations of artificial reproductions of even higher structured tree roots could protect invertebrates even better.

Furthermore, it may be quite challenging but interesting in further studies to repeat the investigations on detachment of invertebrates with smaller individuals of the same species as in the aforementioned experiments I investigated individuals with larger body size since they are more easily visible on the videos. Detachment rates of smaller individuals may vary from the established ones as smaller individuals might on the one hand use also smaller crevices and hiding places more efficiently. On the other hand, smaller and hence younger individuals might be less powerful to fix themselves or resist to shear stress and to return to habitats when displaced.

To conclude, ship-induced waves constitute a direct and immediate disturbance by displacing benthic invertebrates from their habitat. However, the structural complexity of the habitat plays a key role in mitigating ship-induced hydraulic disturbance by providing shelter to benthic invertebrates.

7.3 Subsequent effects of wave disturbance on predator-prey interactions and growth and fitness of invertebrates

The aforementioned studies revealed and quantified the mechanical effect of ship-induced waves on invertebrates, resulting in mass-detachment and dislodgement of individuals. After being detached, invertebrates are hurled through the water column for a while before being able to clink to a habitat again. In the field experiments, some individuals were even drifted away for more than one meter. Hurling through the water column and sojourning in simply structured habitats could mean a higher risk of being preyed upon by fish as dislodged invertebrates might be more easily visible for predators, and open waters and simply structured habitats provide less shelter from predation than complex habitats (Warfe and Barmuta 2004). On the other hand, fish could also be affected by ship-induced hydrodynamic disturbance, too, loosing efficiency in predation. In mesocosm experiments, it was investigated whether

invertebrates face a greater risk of being preyed upon by fish when exposed to continuous wave exposure (simulating natural wind waves) compared to pulsed waves (simulating ship waves) in comparison to a no wave control. Using cross-design experiments, detachment rates of invertebrates as well as fish ingestion rates, swimming and snapping activities for suspended invertebrates of fish with varying body shape were tested. Results showed that invertebrates face a higher risk of being preyed upon by fusiform fish (dace) under wave exposure, while the risk of being preyed upon is diminished in deep-bodied fish, such as bream. These effects were more pronounced under simulated ship waves than under simulated wind waves. Hence, anthropogenic waves may disturb invertebrates more than natural wind waves.

Furthermore, being repeatedly detached could mean that a higher amount of energy is spent for swimming or crawling to return to sheltering habitats for invertebrates. Food consumption might be also more frequently interrupted. In an experimental wave flume, I investigated whether ship waves affect the growth and energy storage of benthic invertebrates. Exposure to artificial ship-induced waves resulted in higher mortality, lower growth, and partially in decreased energy storage of native invertebrates compared to individuals from a no wave control. Hence, hydrodynamic disturbance also affects invertebrate physiology and consequently probably secondary production of littoral zones.

As a consequence of both previous findings, ship-induced waves might lead to lower energy transfer from the invertebrates' trophic level to higher ones. Some invertebrates, noticeably belonging to native species, grew less and gained less weight under wave exposure, partially as they spent more time for swimming. Apart from growing less, they accumulated less energy in their bodies demonstrated by lower glycogen concentrations in their bodies. Hence, in case of *Gammarus roeselii*, individuals ingested a similar amount of energy but could potentially transfer less energy to higher trophic levels. A comparable pattern was also found for *Bithynia tentaculata*, as they also grew less and hence may transfer less energy to higher trophic levels. However, the underlying mechanism was different since *B. tentaculata* individuals did not swim or move more but were observed to ingest less food. Furthermore, for both species survival rate was decreased under wave exposure, eventually leading to lower prey abundance for fish. Thus, results from lab experiments indicated that nutritional resources for fish provided by benthic invertebrates could be reduced at highly wave exposed shores.

Moreover, fish could also be forced to spend more energy to search and catch prey under wave exposure, due to prey rarefaction and hydraulic disturbance, which should finally affect their energy balance. This means that also fish species foraging in invertebrates will transfer

less energy to higher trophic levels. In experimental conditions, deep bodied bream ingested less invertebrates and spent more energy for swimming (Chapter 4) resulting in lower growth rates under wave exposure (Stoll and Fischer 2011). In contrast, one year old dace ingested more invertebrates under wave exposure (Chapter 4) and hence consumed more energy. Stoll and Fischer (2011), however, showed that they are nevertheless not able to convert this energy to increased growth, as they spent more energy for swimming (Chapter 4). Only young dace (0+ age) profited from waves and showed increased growth rates under wave exposure (Stoll and Fischer 2011). Hence older dace and bream which are often among the most abundant littoral fish (e.g. Fischer and Eckmann 1997) might provide less energy for predatory fish, mammals or birds. These effects may aggravate if fish feed on invertebrates which have been exposed to waves for a long time, as prey may become less abundant and prey individuals may be smaller at exposed shores. Concluding, ship-induced waves could result in a loss of biomass and available energy throughout the littoral food web.

However, since only native invertebrates and partially fish are affected by waves, invasive invertebrates and fish might theoretically compensate these effects and substitute reduced biomass production if invasive species are dominating the communities. It may be in fact assumed that some invasive fish might be less affected by ship waves, and thus transfer the same amount of energy to top predators. However, these assumptions are speculative so far, and require further research. A comparative analysis of secondary production and productivity of wave exposed shores and comparison with not exposed sites could provide a deeper insight into effects of waves on energy transfer through littoral food webs.

7.4 Long-term effects of wave disturbance on benthic community composition

The immediate effects of wave disturbance and the subsequent effects on trophic interactions and invertebrate growth or fitness may also lead to long-term changes in the community composition of littoral invertebrate assemblages. Species respond differently to wave disturbance as demonstrated by the contrasted detachment rates observed for different species (Chapters 2 and 3). As a consequence, the structure or the species composition of the littoral invertebrate community is modified, since species are affected differently. Species composition and community structure of benthic invertebrates on the Havel River showed significant differences among exposure levels to ship-induced waves. In contrast to findings of Bishop (2004) from an estuarine environment, total abundances of invertebrates were comparable among exposure levels, but community structure across exposure levels was

different, since abundances of certain species decreased while abundances of some other increased. Hence, species abundances may decrease, increase or level out the same due to wave exposure, which will also result in more indirect effects as biotic interactions might be affected by waves, too.

Many species, especially dragonflies, caddis flies, beetles and snails decreased in abundances with increasing wave exposure. These field observations can be mechanistically explained by direct effects observed in experiments on detachment rates, individual growth and fitness. For example, the aquatic snail *Bithynia tentaculata* was easily detached from sand, while it was able to suck efficiently to the solid surface of stable habitats, thus reducing detachment (Chapter 2 and 3). However, even if not detached from its habitat, repeated exposition to waves resulted in lower feeding rate on suspended particles under wave exposure which in turn lead to lower growth rates (Chapter 5). This is also reflected by decreasing abundances with increasing wave exposure (Chapter 6). Similarly, the dragonfly *Calopteryx splendens*, and particularly the water beetle *Laccophilus hyalinus* showed high detachment rates for most of the habitats under experimental conditions (Chapter 2 and 3). Although these two species were not found at the Havel River, similar detachment rates are to be expected for the dragonflies and beetles species colonizing the littoral zones of the Havel River. Thus, high detachment rates can be directly related to the low abundances recorded on the Havel River at high levels of wave exposure.

Indirectly, repeated exposure to waves may also reduce the abundances of invertebrate predator species by reducing prey availability. This may be true for leech species (Hirudinea) that showed significant reductions in abundances at highly exposed sites. While only a few species can attach their eggs firmly to the substrate, and thus the recruitment of some leech species might be hampered, adult Hirudinea have strong adhesive capabilities (Elliott and Mann 1979). Hence, detachment due to wave disturbance seems to be unlikely for adults. However, Hirudinea are predators or parasites and thus may additionally suffer from reduced prey or host abundances at highly exposed sites (e.g. gastropods, Proctor and Young 1987) which could lead to reduced abundances.

In contrast, some species did not decrease in abundances and some species even increased in abundances with increasing wave disturbance. These species might be directly favoured by waves, e.g. lotic or rheophilic species such as the rheobiont aquatic snail *Ancylus fluviatilis*. Abundances of this aquatic snail tended to increase with increased wave disturbance although occurring only in low abundances (total recorded number of *A. fluviatilis* individuals at highly exposed sites: 312, at intermediately exposed sites 43 and at reference sites: 35 individuals). In

accordance with these findings more lotic species colonized wave-zones of the Great Lakes (Barton and Hynes 1978) and establish a lotic nature of the fauna of the wind wave zone of large lakes.

On the other hand, repeated exposure to waves also indirectly favoured some species that increased in abundance because of decreased interspecific competition or predation. If abundances of predators or dominant species decreased due to hydrodynamic disturbance, abundances of prey or rare species can increase in abundances (Meffe 1984; Leprieur et al. 2006) benefitting indirectly from hydrodynamic disturbance. This might be another reason for the observed strong increase of non-native crustaceans at highly exposed sites of the Havel River, as they seem to be less susceptible to wave disturbance (Chapter 5). Hence, a combination of direct and indirect effects is likely to favour non-native species at highly exposed sites.

These results show that ship-induced waves can profoundly restructure benthic communities. Thereby, waves are not only decreasing individual abundances or species richness, but affect communities in multiple ways via direct and indirect effects.

7.5 Effects of ship-induced waves on non-native invertebrates

Navigation is one of the most important vectors dispersing non-native species, which occurs via hull attachment, ballast water transport or by creating canals which connect water bodies which had previously been separated (Mills et al. 1993; Duggan et al. 2005; Hulme et al. 2008; Leuven et al. 2009). During their migration, which is hence often associated to ship traffic, non-native invertebrates will experience frequent exposure to waves. Thus, successful non-native species managing to colonize new areas via navigational waterways might be, in contrast to native species, only marginally affected by ship-induced waves. The results of this thesis indicate that non-native invertebrates seem to be less susceptible to ship-induced waves than their native counterparts.

For example, the invasive species *Dikerogammarus villosus* was less detached by waves than the native species *Gammarus roeselii* from all habitats apart from roots (Chapter 2 and 3). Furthermore, in contrast to their native counterparts *Dikerogammarus villosus* and the aquatic snail *Physella acuta* were not affected in growth and energy storage by repeated exposure to waves (Chapter 5). In addition, most non-native invertebrate species collected on the River Havel showed similar or higher abundances at shores exposed to ship-induced waves than at not exposed shores while total abundances of native invertebrates decreased with increasing

disturbance of ship-induced waves (Chapter 6). However, it is so far not exclusively clarified if abundances of non-native invertebrates were higher under wave exposure because of a reduced competition by less abundant native invertebrates, or because they prefer to colonize exposed shores. The results of this thesis, however, provide evidence that most non-native species are less susceptible to wave action than their native counterparts. Probably, ship waves might act as an additional trigger for dispersal of non-native invertebrates, and as a selection mechanism which non-native invertebrates have to pass before starting to invade new areas, as most non-native invertebrates spread via navigational waterways where ship waves are present (Mills et al. 1993; Leuven et al. 2009). Anyhow, for potential invader species, invading and colonizing new areas might be hampered in case they are susceptible to wave action. Hence, the ability to cope with wave disturbance might be an important species trait which might favour the invasion success of invertebrates.

7.6 Implications for the management of inland waters

The European Water Framework Directive (WFD) aims to achieve a good ecological status for natural water bodies, and a good ecological potential for artificial and heavily modified water bodies. Most navigational waterways in Europe are classified as artificial or heavily modified water bodies (in Germany 60% of all Federal waterways, Mohaupt/UBA unpubl. data). “Artificial water bodies are bodies of surface water created by human activity” (Article 2(8), WFD, (European Parliament and Council 2000)). “Heavily modified water body means a body of surface water which as a result of physical alterations by human activity is substantially changed in character” (Article 2 (9) (European Parliament and Council 2000)). “Member States may designate a body of surface water as artificial or heavily modified, when: (a) the changes to the hydromorphological characteristics of that body which would be necessary for achieving good ecological status would have significant adverse effects on: (i) the wider environment; (ii) navigation, including port facilities, or recreation” (Article 4 (3(a)) (European Parliament and Council 2000)). However, for 40% of the German Federal waterways a good ecological status has to be achieved. Hence, for these waterways, achieving a good ecological status or potential requires finding a compromise between navigational and ecological needs. For this purpose, profound knowledge on the consequences of navigation on biota and underlying mechanisms is essential to develop sound management plans. The results of this thesis show that ship-induced waves constitute a major disturbance for benthic invertebrates on an individual, species and community level as well as on the interaction between two trophic levels. Hence, ship-induced waves will profoundly affect aquatic

ecosystems. Negative consequences are expected for the functioning of the whole littoral ecosystem. Hence, minimizing wave disturbance should consist in an efficient measure to achieve the good ecological potential required by the WFD. Thereby two basic approaches can be deduced from the described studies to reduce the adverse effects of ship-induced waves on littoral environment: i) Protection measures via shoreline management and ii) Protection measures via navigation management or adaptive development of ships (e.g. ship's hull design) which serve to decrease wave generation, or a combination of both.

Shoreline management should especially aim to protect structural complex habitats as complex habitats such as dense reed stands and submerged tree roots, efficiently dissipate wave energy and provide good shelter for invertebrates, leading to lower detachment rates (Chapter 2 and 3). Furthermore, shoreline protections such as off-bank revetments, parallel breakwaters or shallow areas within the water body may contribute to reduce shear stresses at shores by breaking waves and increasing kinetic energy dissipation (Wolter et al. 2004; Söhngen et al. 2008; Wolter 2010).

Navigation management and boaters' behaviour should aim to decrease the size and frequency of waves produced by navigation, in order to minimize disturbances on invertebrate communities. First, increasing the passing distance of vessels to the shore will decrease wave-induced shear stress at the shores (Chapter 3) hence reducing invertebrate detachments (Chapter 3). Moreover, adjusted vessel speed reduces wave intensity (Bhowmik et al. 1991; Maynord 2005, Chapter 3), Chapter 3). A regulation of the number of boats operating at a certain time will reduce the amount of generated waves, and hence cumulative wave disturbance (Chapter 6). Furthermore, improvements in ship design such as vessel hulls will result in smaller and less energetic waves, and thus could significantly contribute to reduce wave-induced disturbance of littoral environments (Sorensen 1973; Day and Doctors 2001; Söhngen et al. 2008).

7.7 Conclusions

Recreational and commercial navigation are expected to increase in future (Shaw and Loomis 2008; Pauli 2010) and hence the hydrodynamic disturbance of ship-induced waves may increase as well. Ship-waves were demonstrated to comprehensively affect benthic invertebrates influencing multiple and interacting mechanisms (Fig. 20). Increase of ship-induced waves lead on the one hand to higher detachment rates of invertebrates (Chapter 2 and 3), which reduce the growth and energy storage of native invertebrates (Fig. 20). In non-native invertebrates, growth and energy storage are not affected (Chapter 5). In addition, increased

dislodgement may result in a higher risk of being preyed upon by fish if fusiform fish are present. If deep bodied fish are the main predators, the risk of being preyed will be reduced by waves, as deep bodied fish reduce their feeding rate under wave disturbance (Chapter 4).

On the other hand, ship-induced waves favour the degradation, fragmentation and simplification of littoral habitats (Ostendorp 1989 and references therein). Simply structured habitats in turn provide less fixing possibilities and dissipate wave intensities to a lower extent than highly structured habitats and hence increase the detachment of invertebrates. Moreover, simple habitats provide less shelter from predation by fish (Warfe and Barmuta 2004, 2006; but see Mattila et al. 2008) and thus increase the risk of being preyed by fish. Taken together, these mechanisms and relationships will accumulate and may lead to the observed alterations in benthic invertebrate community compositions by among others decreasing species richness and by favouring non-native invertebrates (Chapter 6). Hence, ship-induced waves affect benthic invertebrates at the individual, species and community level, as well as the interaction of trophic levels, and hence might alter whole littoral ecosystems (Fig. 20). These studies elucidate the underlying mechanisms how anthropogenic hydrodynamic disturbance affect benthic invertebrates. This knowledge is essential to understand the effects of ship-induced waves on aquatic ecosystems and to develop scientifically sound management plans for surface waters used for recreational or commercial navigation.

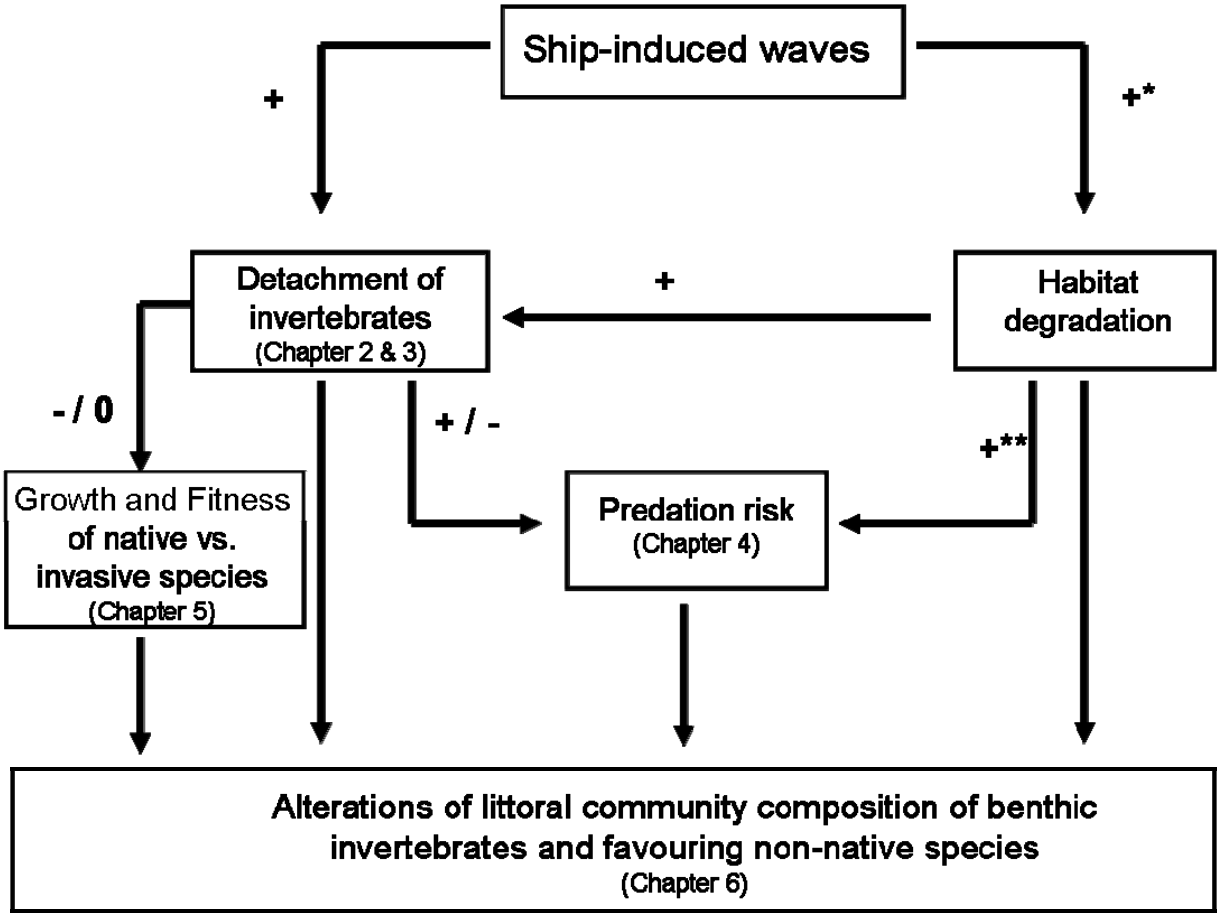

Figure 20: Conceptual model of impacts of ship-induced waves on benthic invertebrates elucidating the underlying mechanisms and relationships leading to comprehensive alterations of benthic communities. * (Ostendorp 1989), ** (Warfe and Barmuta 2004, 2006).

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